

THE MECHANISM OF LOCOMOTION IN SNAKES

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(With Plates 4-6 and Twelve Text-figures)

Among snakes four main types of terrestrial progression have been described: (i) serpentine movement which is observable in all, or nearly all, genera; (ii) concertina movement as briefly described by Wiedemann (1932) in *Vipera* and *Coronella*; (iii) crotaline or 'side-winding' as seen in *Crotalus* or *Cerastes* (Mosauer, 1932*a, b*); and (iv) rectilinear movement as exhibited by boas and other large types (Home, 1812). The observations described in the present paper have all been made on the common grass snake (*Tropidonotus natrix*); the evidence to be presented shows that serpentine, concertina or crotaline movements can all be elicited in this genus by appropriate modification of the external forces operating on the body of the moving animal.

So far as is known, rectilinear movement—in which the animal can progress whilst its body is orientated along a straight line—does not occur in *Tropidonotus*. This type of locomotion depends on active movements on the part of the ribs and ventral scales; such movements have not been seen in *Tropidonotus* whose progression does not depend on active movements of either scales or ribs.

SERPENTINE MOVEMENT

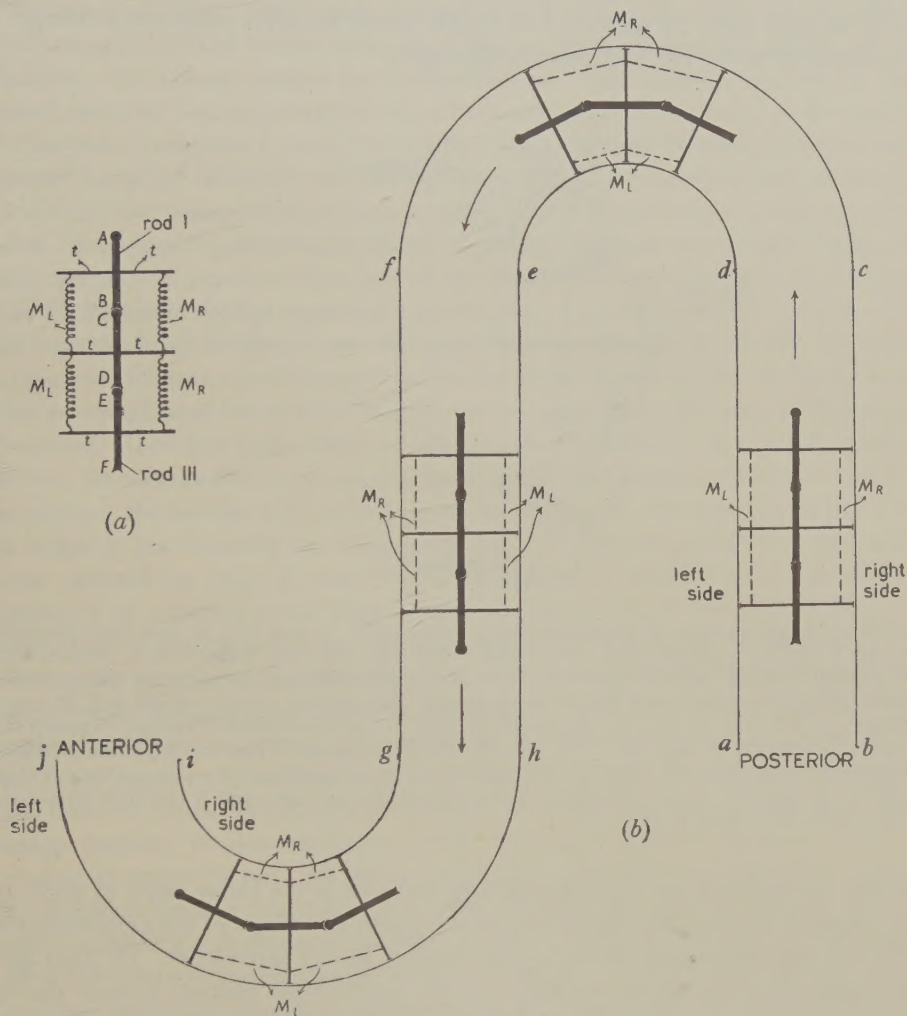
Typical serpentine locomotion is invariably exhibited by *Tropidonotus* when the animal is moving through grass or over a substratum of sufficiently irregular surface. Under such conditions the whole body is thrown into a series of more or less sinusoidal curves, and during movement 'every part of the snake's body and tail faithfully follows the path taken by the head and neck, so that the snake seems to flow gracefully through grass and scrub like a water course in its narrow winding bed' (Mosauer, 1932*a*, p. 585). When the animal ceases to move, all its segments may stop simultaneously; when movement is resumed, all its segments can be set in motion simultaneously. A typical case of serpentine motion is shown in Pl. 4 in which *Tropidonotus* is gliding over a surface of a smooth metal plate from which project a number of smooth glass pegs free to move about their vertical axes only. In essentially the same way the animal can glide over the surface of sand provided this is made sufficiently irregular by the presence of partially embedded pebbles or glass beads. In no case has any exception been found to the conclusion, clearly enunciated by Mosauer (1932*a*), that serpentine motion is strictly dependent upon the presence of projections from the ground against which the body of the animal can be engaged. Since every part of the animal's body is gliding forward con-

tinuously, it follows that all frictional forces operating between the body and the ground must tend to retard the animal's motion and consequently—as also clearly stated by Mosauer (1932*b*)—propulsion must be effected by forces acting normally to the surface of the body; these forces can only be due to the activity of the axial muscles of the body. So far as is known there are no observational studies on serpentine movement other than those of Mosauer which are relevant to the present study. Reference may, however, be made to the physical analysis made by Fokker (1927). This work, published in Dutch, is of a somewhat intricate nature and by no means easy to interpret in biological terms; at the same time, there can be little doubt that its fundamental conclusions—as expressed in the very brief English summary—represent a very important contribution to the theory of serpentine mechanics. From a biological standpoint, however, the fundamental problem is to show how propulsive forces, acting normally to the surface of the body, can be generated by tensions set up in the axial musculature of the body.

From a mechanical point of view, the axial skeleton of a snake can be regarded as a series of rigid rods hinged together to form a chain, whilst the axial musculature can be regarded as a series of elastic elements operating, laterally to the hinges, between adjacent rods. If such elastic elements are to provide the energy necessary for propelling the body, conditions must be such that, during movement, the length of the stretched muscles can decrease. If, for example, a series of such rods and associated elements were confined within a rigid closely fitting channel whose walls were either straight or formed the arc of a circle, the length of the elastic elements would be the same whatever be the position of the system within the channel: in other words, no system of axial elastic elements could move the rods along such a channel. A very simple and instructive test of this fact can readily be applied to *Tropidonotus*: as soon as the animal is confined to a straight or circular channel serpentine motion ceases and is replaced by a totally different type of progression (see Pl. 5 and p. 111). In marked contrast is the ability of the animal to glide through a channel of sinusoidal form (Pl. 6(A)).

In order to visualize the fundamental relationship between the sinusoidal form of the body and the ability of the axial muscles to propel the animal in serpentine movement, it is convenient to consider any three adjacent segments of the body as three rigid rods (*AB*, *CD* and *EF*) hinged together as in Text-fig. 1*a*, each rod possessing transverse processes (*tt*) for the attachment of elastic elements (M_L , M_R) operating about the hinges (*BC* and *DE*). All these elastic elements are assumed to be equal in length and exerting equal tensions. If this system be introduced into the straight, closely fitting and smooth channel (*abcd*) shown on the right side of Text-fig. 1*b*, it can be moved from one position to another within this straight channel without altering the length or potential energy of any of the elastic elements. If, however, the system be moved forward by an external force from the straight section (*abcd*) of the channel to the semicircular section (*cdef*), the elements M_L on the left side of the system can shorten with loss of potential energy, whilst those (M_R) on the right side of the system lengthen, thereby involving an increase in their potential energy. The reverse process occurs when the

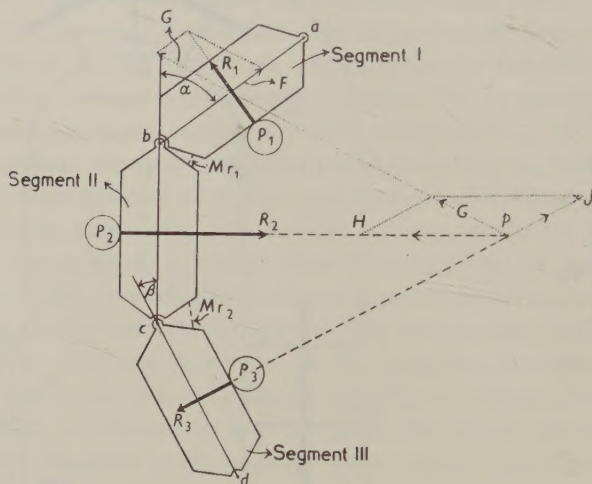
system is moved from the curved section ($cdef$) to the next straight section ($efgh$) of the channel. On moving the system into the second circular section ($ghji$), the elements M_R shorten still further, whilst the elements M_L lengthen, and so on as the system moves through any subsequent sections of the channel. It is clear that each



Text-fig. 1.

elastic element shortens and thereby liberates potential energy whenever the direction of the track or channel changes towards the side of the system on which that particular elastic element is situated relative to the hinge about which it operates; whenever the channel's direction diverges to the left the elements on the left side of the system can liberate energy by shortening, and whenever the channel diverges to the right the same fact applies to the elements of the right side. It is thus possible to establish on quite general grounds the proposition that if a snake confines itself

to—or is confined to—a closely fitting channel or track, any energy stored in the axial musculature can be liberated for locomotory purposes provided that the channel or track is so shaped that it exhibits increasing curvature towards the side of the animal on which the active axial muscles are situated. If each segment of the snake is to use its left and right muscles alternately, it follows that the direction of motion must be restricted to a path which exhibits alternating changes of curvature first to the left and then to the right.

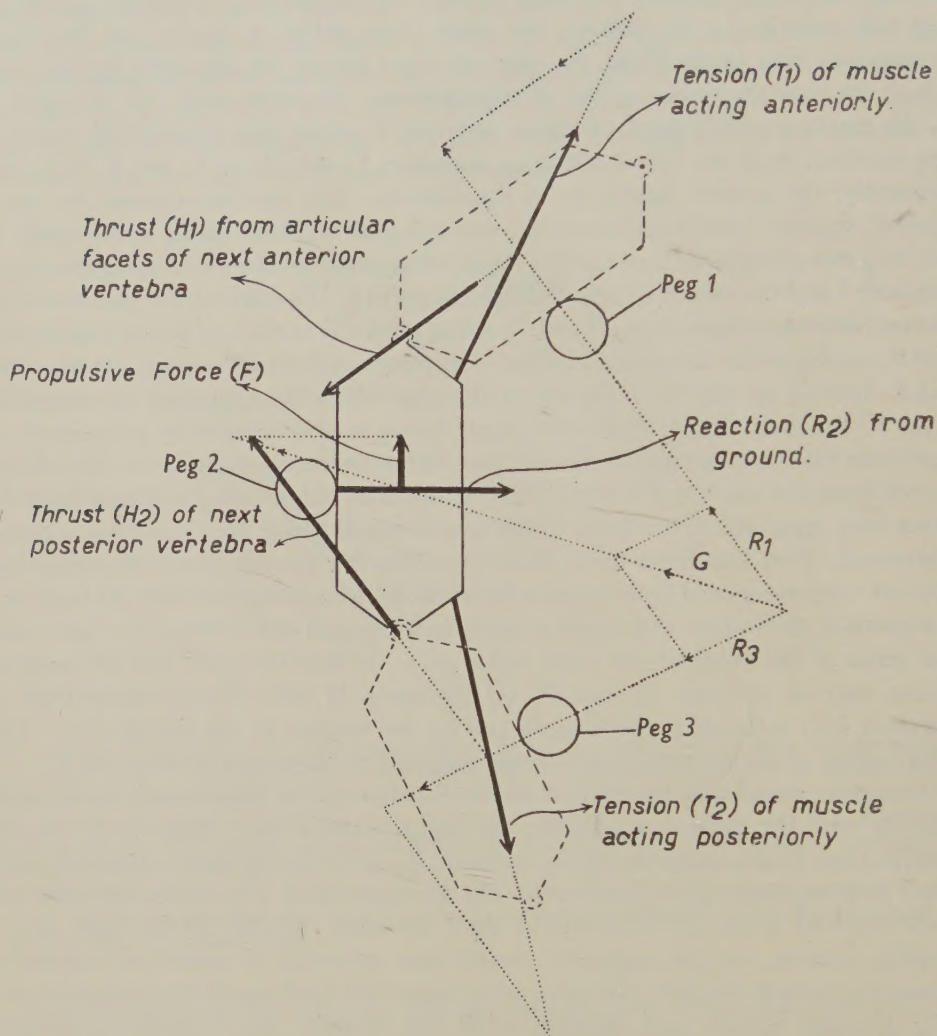


Text-fig. 2. If the posture of three consecutive segments (I, II and III) be such that the angle α (between I and II) is greater than β (between II and III) and each segment is in contact with a rigid resistance (P_1 , P_2 and P_3), forward glide will occur if tension is set up in the elastic elements Mr_1 and Mr_2 acting on the right side of the segments. The reaction of any one peg (e.g. P_1) against the body can be resolved into two components (F and G); the component (F) acting forwards along the axis of segment I is available for the propulsion of the segments past the pegs; the component (G) acting through the point of intersection (p) of the lines of action of the forces acting at P_2 and P_3 can be resolved into forces (H and J) acting along these two lines and is therefore balanced by reactions exerted by pegs P_2 and P_3 .

Before considering the form of a gliding snake from the above point of view, it is convenient to consider the way in which the potential energy of the axial muscles is converted into the kinetic energy necessary for bodily movement. In Text-fig. 2 are shown three successive segments of the body whose posture is such that the longitudinal axis (ab) of segment I forms an angle α on the right of the axis (bc) of segment II, and bc forms an angle β to the right of the axis (cd) of segment III; the angle α being greater than β , the three segments represent a system of increasing curvature towards the right side of the animal. Each segment is in contact at the level of its central transverse axis with a perfectly smooth rigid peg (P_1 , P_2 , P_3), the pegs being arranged as in the figure. Segment I is united to segment II by a rigid element Mr_1 capable of sustaining tension without change in length; segment II is united to segment III by a tensile element Mr_2 which is capable of shortening. So long as Mr_2 is free from tension the rods will exert no pressures against the pegs

and the element Mr_1 will be free from tension. If, however, Mr_2 develops tension, tending thereby to increase the angle β , each segment exerts a pressure against the peg with which it is in contact, but since these points of contact are free from friction, the only forces which the pegs can exert against the segments are reactions which act normally to the surface of the segments. Since the angle α is not equal to β , the reaction which peg 1 exerts on segment I cannot pass through the point of intersection (p) of the forces acting on segments II and III at P_2 and P_3 and, consequently, the system cannot be in equilibrium. Any reaction exerted by peg 1 against segment I can be resolved into two components, both acting at the centre of the long axis of segment I; one (F) of these components acts forwards along the axis of segment I and the other (G) acts through the point p . The latter force can, however, be resolved into components (H and J) acting normally to the surfaces of pegs 2 and 3 and is, consequently, completely balanced by reactions from these pegs. On the other hand, there is no reaction from any of the pegs which can neutralize the tangential force F . Precisely similar arguments apply to any reaction exerted by pegs 2 or 3; in each case the force exerted by any one peg—whatever be its magnitude—can always be resolved into one component which is completely balanced by reactions from the other two pegs, and into a force which acts forwards along the axis of the segment concerned. It is this latter force which provides the driving power for serpentine motion. As soon as this force exceeds the static friction acting between the body and the ground, the former will begin to glide forward, and will continue to move until the angle β has reached the same value as α . It may be noted that the external forces exerted by pegs P_2 and P_3 on segments II and III are transmitted to segment I by a thrust at the hinge b and by the tension of the muscle Mr_1 . The distribution of forces acting on a single segment is illustrated by Text-fig 3.

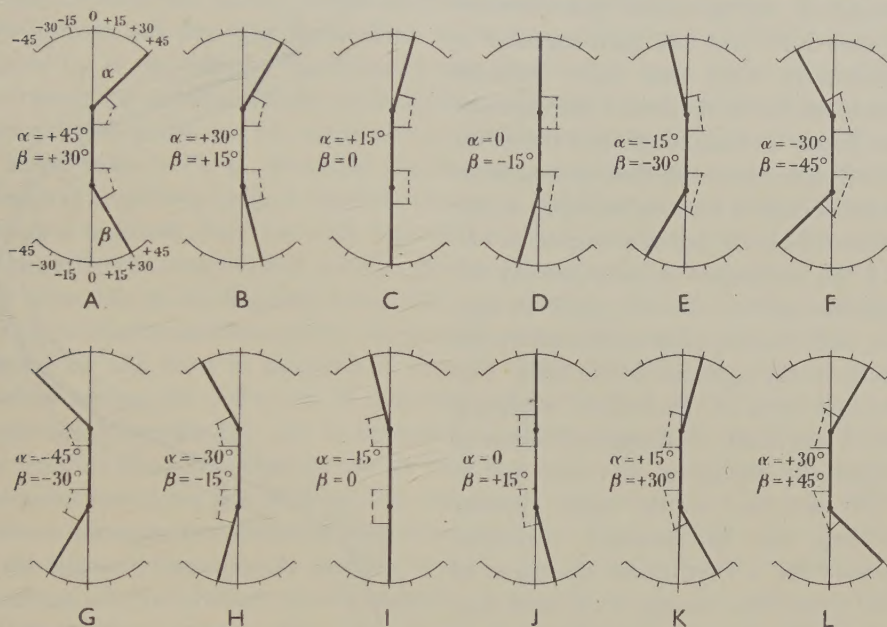
It may be noted that the force available for driving the segments forward varies directly with the difference between the angles α and β (see Appendix I). If α is greater than β , the segments glide forward; if $\alpha = \beta$, the segments remain at rest; if $\alpha < \beta$ the segments glide backwards. On the other hand, if $\alpha < \beta$ the segments will glide forward if the musculature on their left side—instead of the right side—develop tension, for the segments would then represent a system of increasing curvature towards the left. All these conclusions still hold true if the elastic element Mr_1 develops tension and shortens while the element Mr_2 remains of constant length; in other words, forward gliding will occur if both the angles α and β increase—as is the case in a moving snake where each group of muscles shortens and at the same time resists the bending effect exerted on it by its neighbours. The quantitative relationship between the tension of the axial musculature and the force available for propelling the body is considered in Appendix I, but the above facts make it possible to define the essential requirements for active serpentine motion by any short section of the snake's body, namely, (i) the form of the body must be such that the angle which the axis of any segment makes with that of the segment immediately in front of it must be greater than that which it makes with that of the segment immediately posterior to itself, both angles being measured towards the same side of the body; in other words, the posture of the system must be such that the curvature of its anterior



Text-fig. 3. Diagram illustrating the forces, apart from friction or inertia, acting on a single segment of a gliding snake. The tensions (T_1 , T_2) of the axial muscles, together with the thrusts (H_1 , H_2) exerted by the next anterior and posterior segments, exert on the central segment a force (G) identically equal to the resultant of the reactions (R_1 , R_3) from pegs 1 and 3 which act against the anterior and posterior segments. The force G has a component which is compensated by the reaction (R_2) from peg 2 and a forward component F which drives the segment forward. In other words, the driving force represents the resultant component, acting forwards along the median axis of the segment, of all the forces, exerted by the ground against the sides of the snake.

end must be greater than that at its posterior end; (ii) active muscular tension must develop in the axial muscles lying on the side of the body towards which the inclination of the segments or curvature of the body is measured; and (iii) the segments must be subjected to external resistances acting normally to the surfaces of the segments.

Reverting now to the form of a gliding snake it is obvious that the varying curvature of the body is an expression of the fact that the phase of contraction or relaxation exhibited by the muscles varies at different points along the body, the sigmoid or serpentine form being due to the fact that the phase of the muscles operating about any one vertebral joint is slightly further advanced in the cycle of



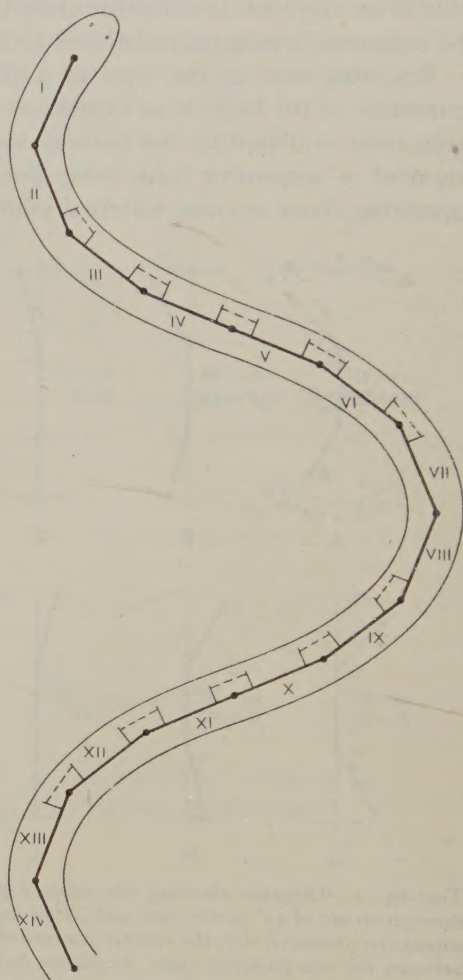
Text-fig. 4. Diagram showing the relative posture of three successive segments each rotating through an arc of 45° to the right and left of its neighbours. The whole cycle is completed in twelve successive phases (A-L); the relative posture of the two anterior rods is always $\frac{1}{2}$ cycle behind that between the two posterior rods. In phases A-F the anterior segment is more inclined to the right of the central segment than is the posterior segment and, consequently, the segments will glide forward if the muscles on the right side of the joints contract. In phases G-L the anterior segment is more inclined to the left of the central segment than is the posterior segment, and consequently the system will glide forward when contraction occurs in the muscles of the left side.

contraction and relaxation than that of those operating about a joint lying slightly anteriorly to itself. Thus if each group of muscles differs in phase from its immediate anterior neighbour by one-twelfth of a complete muscular cycle, any three consecutive segments will exhibit, during one complete cycle of contraction and relaxation, the twelve successive postures shown in Text-fig. 4; between phases A and F (inclusive) the anterior segment is more inclined towards the right of the centre segment than is the posterior segment, and, consequently, all three segments can glide forward provided the muscles on their right sides are active; between phases G and L, on the other hand, the anterior segment is more inclined to the left of the

central segment than is the posterior segment and, consequently, forward glide involves tension and shortening in the muscles on the left side. From the twelve postures shown in Text-fig. 4 it is possible to arrange a series of thirteen successive joints such that the posture of segments I-III is that shown in Text-fig. 4A, that of segments II-IV is that shown in Text-fig. 4B, and so on. In this way the sinusoidal form shown in Text-fig. 5 is obtained. It will be noted that between segments XIV and VII each segment is progressively more and more inclined towards the left of the axis of the segment immediately behind itself, and therefore forward glide can be effected by tension in and shortening of the axial muscles on the left side of the body; between segments VII and I the inclination is progressively towards the right of the next posterior segment, and forward glide is effected by the muscles on the right side of the body. The sigmoidal form of the body of a gliding snake is essentially composed of curves of rhythmically changing curvature first to the left and then to the right, thereby providing the fundamental condition necessary for a rhythmical liberation of useful propulsive energy from each segment by alternating contractions of its right and left musculature.

It is not difficult to construct a dynamic model based on the principles described in this paper, but it is obvious that the form of the animal and its relationship to the environment have been somewhat idealized. It is, therefore, useful to consider in more detail the conditions as they actually exist in a moving animal.

(i) In no case is the amplitude of the muscular contraction, or the difference in phase between successive segments, exactly the same for all segments, nor is



Text-fig. 5. A series of fourteen segments so arranged that the posture of segments I-III corresponds to phase A in Text-fig. 4, that of segments II-IV corresponds to phase B in Text-fig. 3, and so on. Between segments VIII and I the body forms, when measured anteriorly, a curve of increasing curvature towards the right and, consequently, the muscles of the right side can propel the body forwards. From segments XIV-VIII the curvature progressively increases towards the left and propulsion is effected by the muscles on the left side of the body.

the duration of the contraction phase of the muscular cycle necessarily the same as that of the relaxation phase. None of these facts, however, affects the main principle. The

actual form of the body of a gliding snake is an expression of the precise form of the muscular cycle carried out by each group of segmental muscles and of the phase difference between the muscles of successive segments; in every case, however, gliding motion depends on the same fundamental relationship between the position of the contracting axial musculature in respect to an increase in bodily curvature towards the same side of the body. (ii) It has been assumed that each segment of the body is subjected to external restraint which prevents its movement in a direction normal to its own longitudinal axis. In nature, an approximation to such conditions exists when the animal is moving over a surface such as gravel or small stones, or when the animal is moving through close herbage or grass. Again, when moving over soft dry sand (into which the body tends to sink, or which tends to be heaped up at the sides by the animal's own movements) each segment is subjected to a resistance acting normally to its surface. On the other hand, the distribution of external resistances can be restricted to a limited number of points along the body, as is the case in Pl. 4. Precisely similar arguments apply to such conditions if, instead of regarding each of the rods shown in Text-figs. 2-5 as comparable to one vertebral segment, they are each regarded as composed of several such segments. If the system be composed of curved instead of straight units, it can readily be shown that when the muscles acting across any joint develop tension thereby causing the system to exert reactions against the ground at any three points, the forward thrust exerted on the joint in question is directly proportional to the tension in axial muscles and to the difference in curvature of the regions on the two sides of the hinge (see Appendix II). (iii) In the idealized system represented in Text-figs. 2-5, it is possible to assume that the energy liberated, when the muscles operating across each joint pass from one phase of the contraction cycle to the next, is just sufficient to move the segment concerned from its original position to that previously occupied by the segment immediately anterior to itself. In a living snake this condition is by no means always fulfilled; more frequently, some regions provide some or all of the energy required to move other parts of the body. The fundamental principles are, however, unaffected, although the actual work done by any particular part of the body can only be determined by experimental methods which will be discussed in another paper.

From a biological point of view, the rate of progression of a snake depends on the rate at which the animal moves along its own axis of symmetry—in other words, on the wave-length of its sinusoidal track rather than on the rate at which a segment glides along the track itself. For rapid progression, the curvature of the body should be such as to provide curves of long wave-length and low amplitude. For this purpose, the amplitude of the muscular contractions and the phase differences between adjacent segments should both be small; curves of this form would, however, yield relatively small propulsive components, and would therefore require greater muscular effort. It would be of considerable interest to consider the relationship of the forms of the body in different genera in relationship to their speed of locomotion.

Before leaving serpentine movement it may be noted that the propulsive mechanisms of a gliding snake and of an eel moving through grass are essentially

the same; the smooth surface of the eel with its associated mucus reduces friction to a minimum and is therefore ideally adapted for serpentine movement. The analysis of serpentine movement given above can readily be modified to cover conditions under which friction acts against the sides of the snake whenever these are pressing against the ground; the greater the coefficient of friction, the greater is the tension of the muscles necessary to propel the animal.

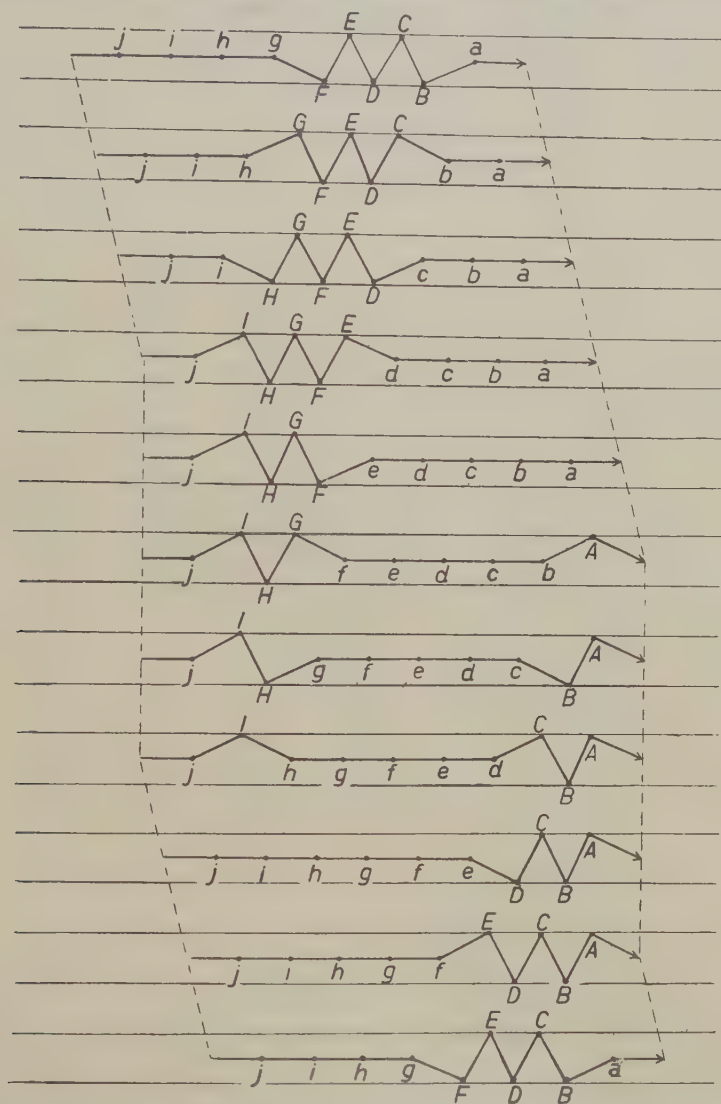
CONCERTINA MOVEMENT

As already mentioned, the type of movement exhibited by a snake when confined within a channel whose walls are either straight or form the arc of a circle differs strikingly from that exhibited within a channel of varying curvature. In a straight or circular channel, locomotion is effected by highly characteristic concertina movements illustrated by Pl. 5, from which it can be seen that the body is thrown into a number of curves, of comparatively short wave-length, which are in contact at their crests with the walls of the channel; as the cross-section of the channel is decreased so the number of curves exhibited by the body increases, whilst, at the same time, their wave-length decreases. Reference to Pl. 5 shows that the segments of the body which constitute a fully developed wave constitute regions which are at rest relative to the walls of the channel, whereas segments are in motion when they lie on regions where the curvature is being increased or decreased. Each fully formed wave represents a rigid structure firmly pressed against the wall of the channel, thus forming a *point d'appui* towards which (or away from which) the moving regions can be drawn against the sliding friction of the floor of the channel.

The kinematics of motion are shown in Text-fig. 6 in which capital letters denote points on the body which are in firm contact with the walls of the channel whilst regions in motion are shown by smaller letters. As motion proceeds, fresh *points d'appui* are established behind existing ones, whilst the segments which constitute the most anterior of the wave series are drawn away from the walls of the channel and begin to move forward. It will be noted that each segment, in turn, comes to rest and then moves forward, thus executing definite and discrete steps.

The pattern of muscular effort and the distribution of external forces acting on the body during concertina movement are shown in Text-fig. 7*a*, in which the sections of the body *cd* and *de* are locked to the sides of the channel at *c*, *d* and *e* by virtue of the tension in the muscle *Md* operating between *cd* and *de*. The forward movement of the anterior end of the body is due to (i) an unlocking action at *c* due to contraction of the muscles (*Mc*) operating on the right side of hinge at *c*, and (ii) contraction of the muscles *Ma* and *Mb* operating to the right and left of their respective hinges *a* and *b*. Similarly, the forward movement of the region of the body posterior to *e* is due to the shortening of the muscles *Me*, *Mf* and *Mg*. In order that the animal should propel itself through the tube, the static friction (Text-fig. 7*b*; *Fc*, *Fd* and *Fe*) operating between the body and the tube at *c*, *d* and *e* must be equal to the total sliding friction (*Fh* and *Ft*) of all parts of the body which are in motion, so that the pressures (*Pc*, *Pd* and *Pe*) exerted on the animal

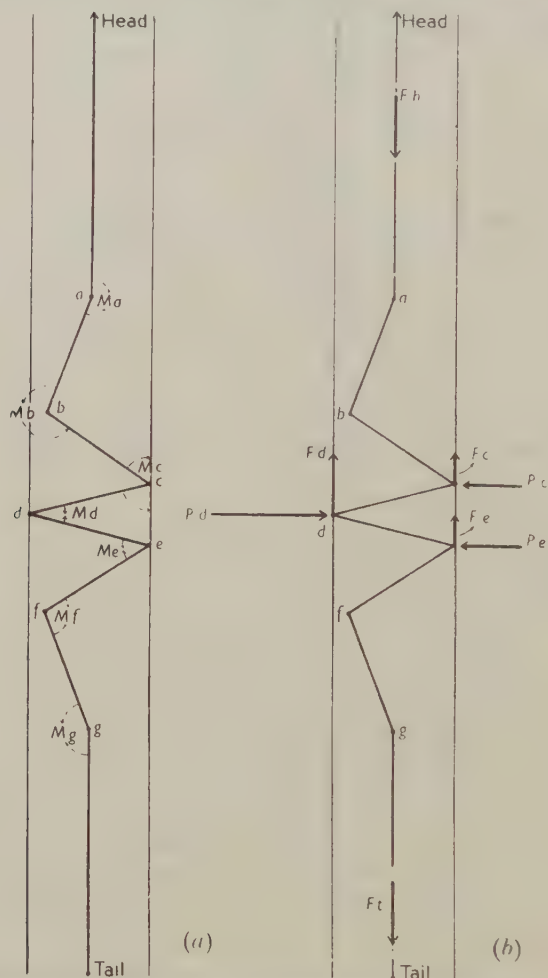
normally to the sides of the channel must be such that at none of the points *c*, *d* or *e* is the ratio of friction to pressure in excess of the coefficient of friction.



Text-fig. 6. Diagram illustrating the movement, relative to the ground, of a snake during concertina movement through a straight tube. Capital letters indicate regions of the body at rest; smaller letters indicate regions of motion. Each segment of the body moves forward in a series of distinct steps.

Although concertina movement is highly characteristic of snakes moving in channels of straight or circular form, it nevertheless sometimes occurs in a somewhat modified form when a snake is moving over open ground of fairly uniform surface. An example of this is given in Text-fig. 8. This type of movement depends on the fact that movement of a series of segments backwards along their own

longitudinal axis causes the posterior edges of the ventral scales to engage passively with the surface of the ground and so enables such segments to act as a *point d'appui*. The force required to tow an inert *Tropidonotus* linearly backwards is four

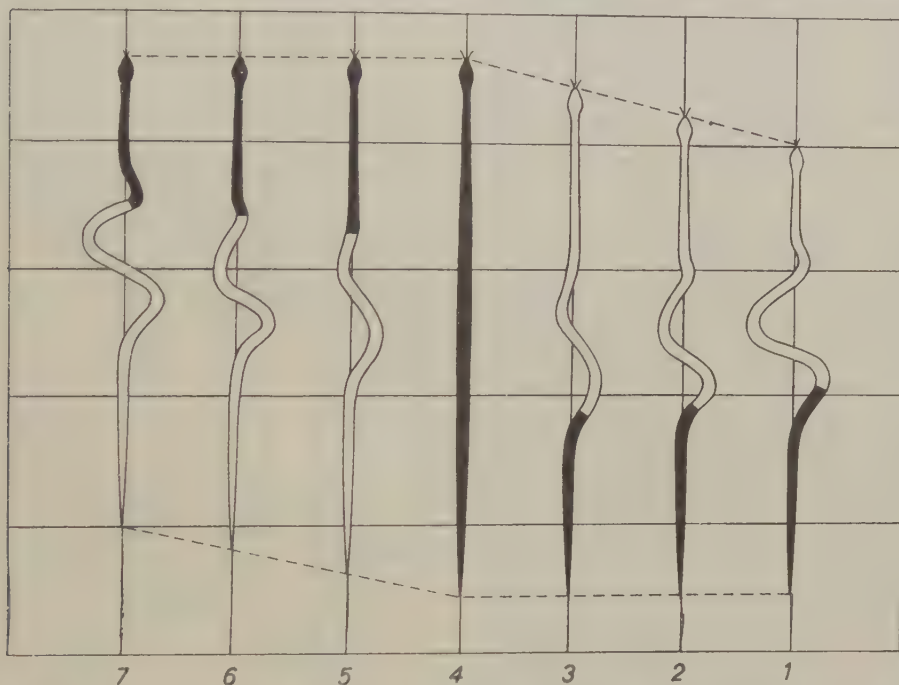


Text-fig. 7. *a*. Diagram illustrating the mechanism of concertina movement in a straight tube. The sections of the body *cd* and *de* are locked against the walls of the tube by contraction of the muscles *Md*; the region of the body anterior to *c* is being extended forwards by contraction of the muscles *Ma* and *Mc*, operating about the right side of joints *a* and *c*, and of *Mb* about the left side of joint *b*. The region of the body posterior to *e* is being drawn forward by contraction of the muscles *Mf* and *Mg*. *b*. Diagram illustrating the external forces acting on the body during concertina movement. *Pc*, *Pd* and *Pe* are the forces exerted by the walls of the tube normally to its surface at *c*, *d* and *e*; *Fc*, *Fd* and *Fe* are the frictions acting anteriorly to *c*, *d* and *e*; *Fh* and *Ft* are the sliding frictions between the floor of the channel and the anterior and posterior ends of the body respectively.

or five times greater than that required to tow it forward even if the substratum is relatively smooth; if active concertina movements are restricted to the central half of the body, the regions in front of and behind the active region can act alternately as efficient fixed *points d'appui* as in Text-fig. 8.

CROTALINE OR SIDE-WINDING MOVEMENT

When a grass snake moves over a relatively smooth and uniform surface its mode of progression tends to be irregular, and serpentine movement is replaced either by side-winding, or by concertina movement, or a combination of the two. The precise mechanical conditions of the substratum necessary for the elicitation of side-winding in its most characteristic form cannot be defined at present, but an instance is shown in Pl. 6 (C), in which the animal is moving over a painted metal plate; Text-fig. 9a shows the movement, relative to the ground, of the animal seen in



Text-fig. 8. Successive phases (1-7) in the concertina movement of a snake not subjected to any lateral restraint, but in which curvature of the body is restricted to the central region of the body. Regions of the body at rest are shown in black. Progression is due to the passive action of the ventral scales whose free posterior edges cause the static resistance to a backward displacement of the body to be four or five times greater than that to forward displacement.

Pl. 6 (C). During this type of progression two sections of the snake's body remain at rest relative to the ground, whereas the remainder is in motion (Text-fig. 9b); consequently, the whole body moves sideways in essentially the same way as was described by Mosauer (1932 *a, b*) as the normal method of progression in the 'side-winder' (*Crotalus cerastes*) or for the sand-vipers (*Cerastes cornuta* and *C. vipera*).

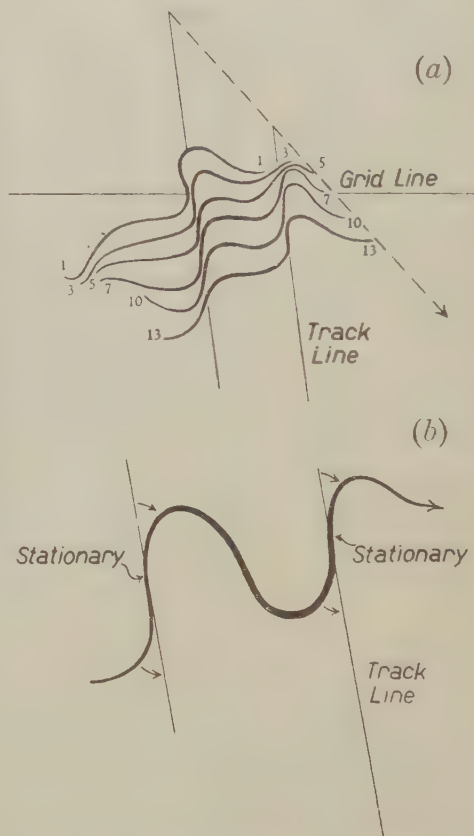
Although a good description of crotaline movement has been given by Mosauer, it is perhaps convenient to recall its essential features before considering the kinetics of this type of movement. A side-winding snake leaves on the ground a series of more or less parallel straight tracks inclined at an angle to the path of motion of the animal's head. These tracks represent lines along which each segment

of the body is placed, in turn, and from which it is, in due course, lifted in order to be moved to the next track in the series. Segments of the body actually lying on the track are at rest relative to the ground, segments lying immediately anteriorly to those at rest are being lifted off the track, whilst segments lying immediately posteriorly to those at rest on the track are being placed down (Text-fig. 9*b*)—the terms anterior and posterior being used relative to the head of the animal. The whole cycle is essentially similar to that of the treads of a caterpillar drive of a tank or tractor. During crotaline movement, contact between the body and the ground is, to a very large extent, restricted to segments of the body which are lying at rest on the rectilinear tracks but the inability of *Tropidonotus* to side-wind over sand-paper shows that at least some of the moving segments must, in this form, be in contact with the ground.

The mechanical relationship of side-winding to serpentine motion is simple; it depends, primarily, on a difference in the external forces which oppose the contraction of the axial muscles. At the lower right side of Text-fig. 10 is shown a series of twenty-four segments whose positions relative to each other are exactly comparable to those of the fourteen segments shown in Text-fig. 5. If adequate lateral resistances and muscular effort are available, the whole series of segments would, during two complete muscular cycles, glide by serpentine movement along the sigmoidal track (H_1-H_7) which traverses the horizontal line at the base of the figure. On the other hand, if the external

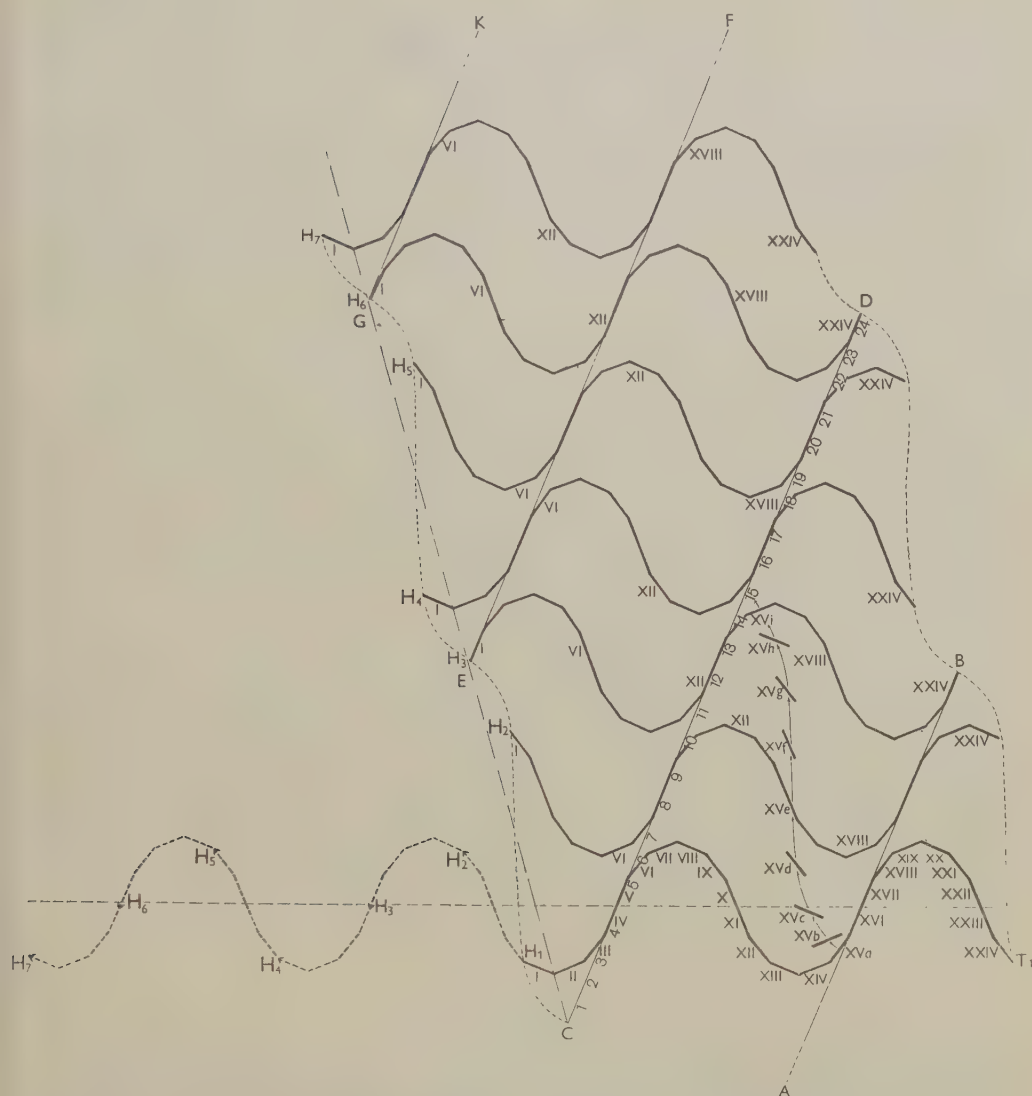
resistances are such as to allow unrestrained movement to each segment except at the end of each complete cycle of movement (as defined by the phase at which the segment subtends no angle with the axis of either the segment in

front of or behind itself) the displacement of the animal relative to the ground, during two complete muscular cycles, is shown in Text-fig. 10 by the six postures seen above the original position of the animal. When movement starts, segment V remains at rest whilst segment IV is deflected towards the morphologically right



Text-fig. 9*a*. Diagram showing successive positions of the animal shown in Pl. 6 (C), relative to a fixed grid line; the numbers correspond with those in the Plate.

Text-fig. 9*b*. Diagram showing the motion of various regions of the body relative to the track lines during crotaline movement.



Text-fig. 10. Diagram illustrating the relationship of side-winding to serpentine motion. If adequate external resistances act normally to the surface of the twenty-four segments shown at the lower right side of the diagram, the animal will glide to the left from its initial position ($H_1 T_1$) along the sinusoidal track (H_1-H_7) traversing the horizontal dotted line shown at the lower left side of the figure. If, on the other hand, all segments are unrestrained by any external forces except when they are in the phase shown by segments V and XVII in the animal's initial position at $H_1 T_1$, then the animal will side-wind towards its right side; the head of the animal moves along a curve whose axis is CEG . Each segment in turn comes to rest on one of the track lines (AB, CD, EF, GK) and is subsequently moved to the next track line in the series. The movement of an individual segment, during one complete muscular cycle, is shown in the case of segment XV when moving from track line AB to track line CD .

side of segment V; simultaneously, the angle between segments V and VI is reduced until segment VI comes to rest with its axis in line with that (*CD*) of segment V. Similarly, segment XVII remains at rest whilst segment XVI moves to the right of the axis (*AB*) of segment XVII, whilst segment XVIII moves to its position of rest on this axis. As the muscular cycle proceeds, segments VII, VIII, IX, ... are laid down along the line *CD* and segments XIX–XXIV are laid down along the line *AB*; simultaneously, segments which have previously been at rest along these lines are lifted and moved forward towards the next track line of the series; the movement, relative to the ground, of one such segment is shown in the case of segment XV from its position *XVa* on the track line *AB* to *XVi* just before taking its place on track line *CD*. It will be noticed that the total length of each track line is the same as the length of the animal; the track lines will only be parallel to each other throughout the whole of their course if the amplitude of the muscular movements and the phase difference between adjacent segments are the same along the whole body. A good illustration of actual track lines is given by Mosauer (1928).

The ability to side-wind depends on the ability of the snake to transfer some or all of its weight to the segments which are to remain at rest, thus increasing static friction at these points and reducing or abolishing the sliding friction of the regions of the body which are in motion; this is effected by rhythmical changes in tension in the dorso-ventral axial musculature.

According to Mosauer (1932*a*) the substratum of a true side-winder does not provide a propulsive force necessary for progression. This can only be true under theoretical conditions where movement is occurring at a perfectly uniform speed and when all the moving parts are out of contact with the ground. Unless static friction operates posteriorly between the ground and the stationary segments, the animal could not start from rest—for the whole body would slip freely over the ground as is the case when the animal is on an extremely smooth plate; further, if any external restraining force acts on the moving segment, a corresponding amount of friction must act posteriorly on the segments lying at rest on the ground.

APPENDIX 1

The propulsive effect of reactions acting normally to the surface of the body can be visualized quantitatively from Text-fig. 11 in which *ac* is a rigid angular bar in contact with two smooth pegs P_1 and P_2 and hinged at *c* to a straight rod *cd* which is in contact with the peg P_3 ; an elastic element *Mr* acts on the right side of the hinge at *c*.

If the tension of the element *Mr* be *T* and its moment about the hinge be Tz , the two rods will be exposed to equal and opposite turning couples of moment Tz ; the reaction (R_3) of peg 3 against *cd* will be Tz/x .

If *F* is the external friction, forward glide at constant speed can occur when the resultant of R_1 , R_2 and R_3 is equal but opposite to *F*; in other words when

$$F = R_1 \sin \alpha - R_3 \sin \beta,$$

$$R_2 = R_1 \cos \alpha + R_3 \cos \beta,$$

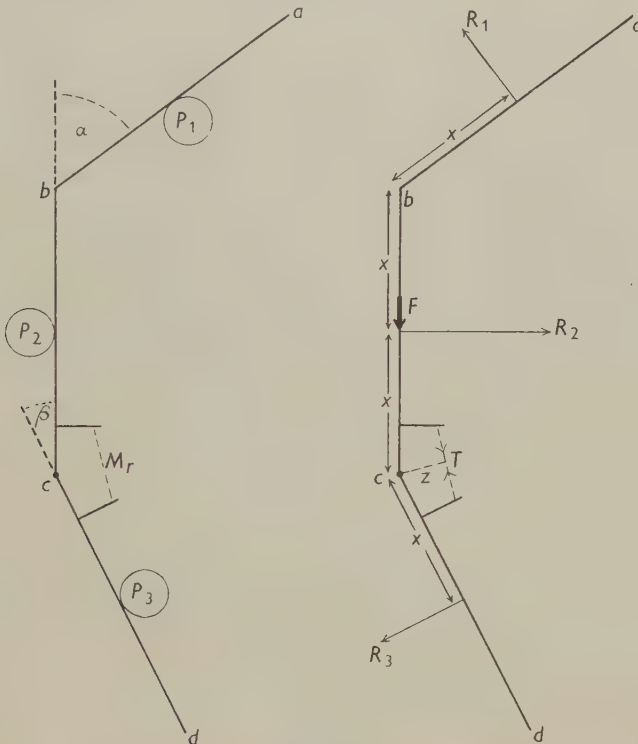
$$R_2 = R_3 (1 + 2 \cos \beta) - R_1.$$

Under such conditions the force tending to drive the animal forward is equal but opposite to F and has the following value:

$$\frac{Tz}{x} \left[\frac{\sin \alpha - \sin \beta + \sin (\alpha - \beta)}{1 + \cos \alpha} \right].$$

If $\alpha = \beta$, F becomes zero—as when a snake's body is in the form of the arc of a circle or lying along a straight line.

If $\alpha > \beta$ the animal must glide forward if the axial muscles develop tension on the right side of the body towards which side α and β were measured. If these muscles became active when $\alpha < \beta$ the animal would glide backwards.



Text-fig. 11.

If $\alpha < \beta$ and the muscles on the left side develop tension the animal would glide forward.

If a muscle (Mr) acting about a joint at c shortens, the muscles acting about b (on the same side of the body) must resist the bending moment of Mr and vice versa. In life both groups of muscles shorten and each contracts against the bending forces induced by the other.

It may be noted that the propulsive force represents the sum of those components of the reactions from all three pegs which acts along the axis of the central segment in Text-fig. 3.

APPENDIX II

Let AB be a region of the snake's body such that the radius of curvature between B and H is r_2 , whilst that between A and H is r_1 , r_2 being greater than r_1 (Text-fig. 12). At H , the

bending moments which must be resisted by the muscles of those segments of the body not in contact with the pegs:

$$R_1 = \frac{Tz}{r_2 \sin \alpha},$$

$$R_2 = \frac{Tz[r_2 \cot \alpha + r_1 \cot \gamma]}{r_1 r_2 [\cos \beta - \sin \beta \cot \gamma]},$$

$$R_3 = \frac{Tz[r_1 \cos \beta + r_2 \cot \alpha \sin \beta]}{r_1 r_2 \sin \gamma [\cos \beta - \sin \beta \cot \gamma]}.$$

SUMMARY

1. Of the four main types of locomotion observed in snakes, three (serpentine, concertina and crotaline) can be elicited from the common grass snake (*Tropidonotus natrix*) by appropriate modification of the animal's environment.

2. Serpentine motion depends on three factors. (i) The body must be thrown into one or more curves each of which exhibits an increase of curvature when measured towards the head of the animal. (ii) Active muscular tension must develop in the axial muscles which lie on the same side of the body as that in which the curvature is increasing. (iii) The body must be subjected to at least three external resistances acting normally to the surface of the body. The propulsive force is the resultant of the reactions exercised by all these external resistances.

3. A snake cannot propel itself by serpentine movement along a straight or circular path. Under such conditions *Tropidonotus* progresses by concertina movements, the nature of which are described.

4. The muscular cycle of a snake exhibiting 'crotaline', or side-winding, movements is essentially the same as that during serpentine motion; the difference in the type of movement relative to the ground is due to a difference in the nature of the external resistances offered by the animal's environment. The mechanical principle of crotaline movement is, fundamentally, that of a caterpillar tractor.

5. Serpentine, concertina, and crotaline movements do not depend on active movements on the part of the ribs or scales. Rectilinear movement involving these structures has not been observed in *Tropidonotus*.

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EXPLANATION OF PLATES

PLATE 4

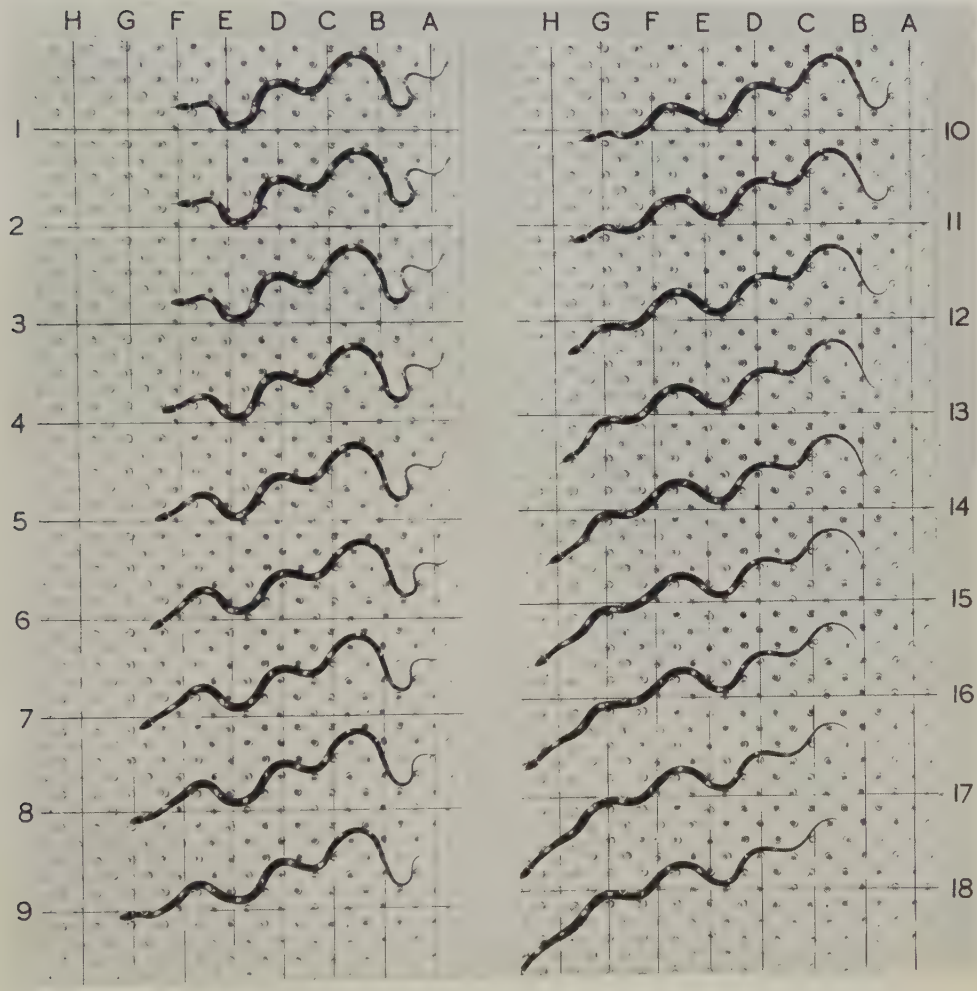
Eighteen successive photographs of a snake (*Tropidonotus natrix*) gliding over a smooth plate from which project a series of rigid pegs. The vertical lines *A-H* and the horizontal lines 1-18 are drawn through the same pegs in all the photographs. The progress of the animal can be followed by noting the successive position of any one of the white spots, painted on the back of the animal, relative to the grid lines. For example, the spot which, in photograph 1, lies about midway between grid lines *B* and *C*, has, in photograph 18, passed beyond grid line *E* by following a path which is defined by the form of the body as seen between lines *B* and *E* in photograph 1. Note that the animal starts to move soon after photograph 2. Interval between successive photographs 0.25 sec.; distance between vertical grid lines, approx. 3 in.

PLATE 5

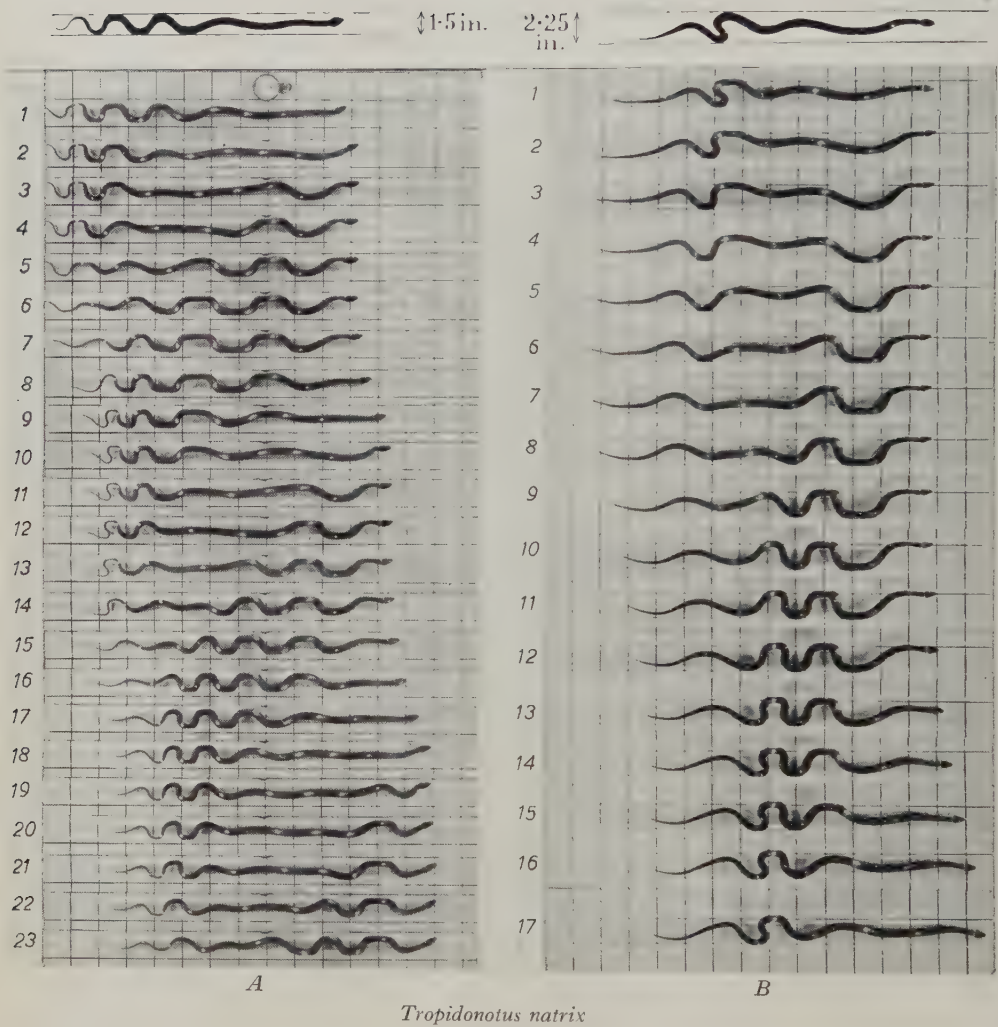
'Concertina' pattern of movement displayed by *Tropidonotus natrix* when confined within a straight glass tube. The diameter of the tube is shown by the drawing at the top of each series of photographs. Interval between successive photographs, in series A, 0.25 sec.; in series B, 0.5 sec. Distance between vertical grid lines 2 in.

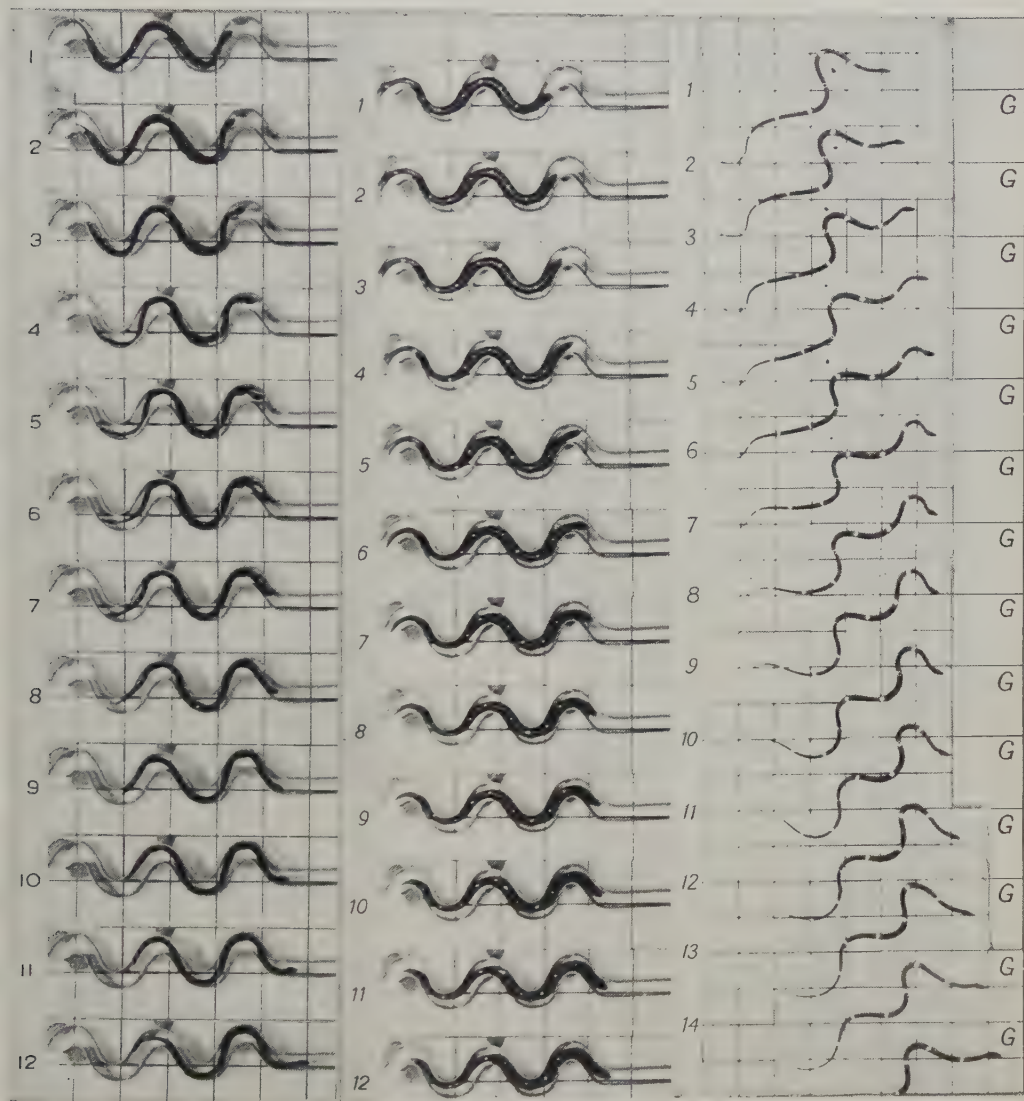
PLATE 6

A. Serpentine movement of *Tropidonotus natrix* through a channel of varying curvature. Interval between successive photographs 0.25 sec. Distance between vertical grid lines 2 in. B. Serpentine movement of a slow-worm (*Anguis fragilis*) through a channel of varying curvature. Interval between successive photographs 1.5 sec. Distance between vertical grid lines 2 in. C. Side-winding movement of *Tropidonotus natrix* when moving over a metal plate. Interval between successive photographs 0.2 sec. Distance between vertical grid lines 2 in. For displacement of the body relative to the ground see Text-fig. 9a.



Tropidonotus natrix





FURTHER OBSERVATIONS ON THE EFFECT OF DE-AFFERENTATION ON THE LOCOMOTORY ACTIVITY OF AMPHIBIAN LIMBS

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(With Four Text-figures)

The extent to which co-ordinated rhythmical patterns of locomotory movement are to be regarded as expressions of intrinsic activity within the central nervous system, and how far they are dependent upon the patterns of impulses received from peripheral sense organs, remains a fundamental problem in general physiology. In previous communications we have discussed this problem with reference to the ambulatory activity of Amphibia (Gray & Lissmann, 1940). We found that when the limbs and body of a toad (*Bufo bufo*) are desensitized by severance of their sensory nerves, the effect on the locomotory pattern depends to a very marked degree upon the extent to which the process of de-afferentation has been applied to the whole of the somatic musculature. In conformity with the results obtained by previous investigators (Hering, 1893; Weiss, 1936) we found that de-afferentation of either one or two limbs did not substantially affect the co-ordinated, diagonal pattern of limb movements. When three limbs were de-afferentated the ambulatory activity of the animal was substantially reduced; nevertheless, the diagonal co-ordination of the limbs was maintained whenever movement occurred. When four limbs were de-afferentated, ambulation was laboured and restricted to a few steps at a time. On the other hand, when de-afferentation was applied to all the spinal nerves II–XI (inclusive) no trace of ambulatory rhythm or of diagonal limb movements was observed, although non-ambulatory responses were obtained from the limbs by labyrinthine or optical stimulation. From these observations we were unable to derive any positive support for the theory, advocated by Weiss (1936), that the power to maintain rhythmical ambulatory limb movements is an intrinsic property of the central nervous system and fundamentally independent of the peripheral sense organs. We see no reason to amend our views, but further consideration is desirable in view of the subsequent publications by Weiss (1941 *a, b*) which not only stress the conception of an inherent central nervous control of ambulatory rhythms but quote our experiments in its support.

A. THE EFFECT OF COMPLETE SPINAL DE-AFFERENTATION ON AMBULATORY CO-ORDINATION

Although severance of the dorsal roots of spinal nerves II–XI on both sides of the body of a toad effectively desensitizes the whole of the normal ambulatory musculature, it is necessary to note that considerable variation exists in the number, size and

position of the individual nerves, particularly of those associated with the posterior end of the spinal cord. Not only may the dorsal root of XI be enclosed for a variable distance in the same connective tissue sheath as that of X, but on some occasions a XIIth spinal nerve may be present. Both XI and XII may be very small, and the only satisfactory test of total de-afferentation in the posterior region of the body is provided by careful post-operative tests for local sensitivity.

In all our experiments de-afferentation has been effected by the following technique. The toad was anaesthetized by ether, firmly fixed in an operating dish, and the skin opened by a dorsal median incision extending from the back of the skull to the anterior end of the urostyle. The dorsal aspect of the vertebral column was exposed by dissecting away the vertebral region of the longissimus dorsi, and by detaching, in the shoulder region, muscle fibres inserted on the dorsal side of the vertebrae (rhomboideus posterior, latissimus dorsi, etc.). The neural arches were then cut on each side, with a fine dental separating saw, about 1 mm. laterally to the neural spines; the spinal cord was exposed by removing this bony roof and the membranes covering the cord. In some instances slight bleeding was unavoidable at this stage. By subjecting the cord to a fine jet of saline or Ringer solution the dorsal and ventral roots of the cauda equina could be spread out and severed without much difficulty. Least accessible are the ventral roots of the 'hypoglossal' (II) and of the anterior spinal nerves. In cases where the dorsal roots of these nerves had to be left intact, a fine, hooked insect needle was inserted into the neural canal, laterally to the cord and below the corresponding dorsal root. The ventral root was caught with the hook, gently pulled up, and cut with spring scissors. After the operation the skin was closely stitched up. The animals survived well, and in the later stages of this investigation very few casualties occurred.

Altogether we have examined the behaviour of twenty-five animals after complete de-afferentation of their spinal nerves; in twelve of these, bilateral de-afferentation applied to spinal nerves III–XI abolished all signs of ambulatory co-ordination. In the other thirteen animals de-afferentation was applied to nerves II–XII; in twelve of these no sign of ambulatory co-ordination remained, but the thirteenth animal very occasionally displayed an alternation of limb movements which might be regarded as comparable to that displayed by the toad observed by Weiss. It is however significant that in our specimen the deeper tissues of the shoulder (supplied by cranial nerve X) showed an unusual degree of sensitivity to external stimulation; further, the movements of the limbs were always accompanied by marked movements of the head. For reasons to be given elsewhere it seems not improbable that the limb movements of this animal may also be related to stimulation of labyrinthine origin. Apart from this single, somewhat ambiguous exception, all our observations emphasize the dependence of the ambulatory rhythm on the integrity of a small but finite amount of the peripheral nervous fields.

The most striking feature of these experiments is the marked effect of the presence or absence of one, relatively small, region of the ambulatory musculature whose sensory and motor nerve supply is intact. Just as complete absence of true ambulatory movements is the characteristic feature of an animal which has been de-

afferentated in respect to all its spinal nerves, so a definite though variable amount of diagonal limb movement is characteristic of an animal in which one segment of the body is intact in respect to both its sensory and motor nerves.

It is not possible to give a quantitative estimate of the intermediate levels of co-ordinated behaviour which lie between the two extremes of normal ambulation and complete absence of diagonal limb movements. The intermediate levels (characteristic of varying degrees of de-afferentation) have been described qualitatively elsewhere (Gray & Lissmann, 1940) and observation of a large number of animals has indicated very clearly the progressive loss of co-ordinated ambulatory activity with advancing stages of de-afferentation. Further, it is the extent and not the site of de-afferentation which is important. The number of fibres in dorsal roots V-VII collectively appears to be approximately equal to that in the dorsal roots of VIII. There is, however, no appreciable difference in the ambulatory activity of animals which retain roots V-VII from that displayed by animals retaining VIII; both types display clearly defined periods of diagonal ambulation. As reported in our previous paper (1940), one or more intact dorsal roots are only capable of sustaining ambulation provided that their associated motor roots are intact. A decisive demonstration of this fact is provided by a toad in which all the spinal dorsal roots were severed with the exception of IX and X supplying the left hindlimb; after this operation the animal exhibited well-defined diagonal ambulation in response to tactile stimulation applied to the intact limb. The ventral roots IX and X of the left hindlimb were then severed. After this second operation tactile stimulation of the left hindlimb invariably evoked a characteristic monophasic response in each of the three limbs; no sign of ambulation could be elicited. It therefore seems difficult to avoid the conclusion that ambulation depends on the existence of sensory impulses arising in the ambulatory musculature.

B. THE EFFECT OF DE-AFFERENTATION OF A SINGLE LIMB AFTER DE-AFFERENTATION OF THE REMAINING LIMBS AND BODY

Whilst the results of de-afferentation do not provide positive evidence in support of central determination of the ambulatory rhythm they do not disprove it. It is possible that extensive de-afferentation so depresses the excitability of the central nervous system as to render it incapable of displaying its normal activity. In order to explore this possibility, use has been made of preparations in which three of the limbs and the body of a toad are immobilized by severance of their motor roots whilst the fourth limb is, at first, intact but is subsequently de-afferentated. Preparations of this type were examined as follows.

After opening the spinal canal and severing the appropriate roots the animal was mounted on a moist glass plate in such a way as to permit freedom of movement for the intact limb. Subsequent to recovery from the anaesthetic, the application of relatively weak stimuli to any of the de-efferentated limbs elicited clearly defined ambulatory movements in the intact limb, the excitability being not substantially lower than that required to elicit a response in the intact animal. This observation shows that so far as the movements of the intact limb are concerned, the excitability

of the central nervous system has not been seriously reduced by cutting off all the sensory impulses which may normally arise in the muscles of the other three limbs. Typical responses are illustrated in Figs. 1-3. In Figs. 1 and 2 the right posterior limb was initially intact, whilst the other hindlimb was immobilized by de-efferentation, and the body and forelimbs were totally denervated. On applying a series of condenser discharges (Fig. 1, tracing (a)) of appropriate strength to the plantar surface of the left posterior limb, the intact right posterior limb responded by a clearly defined rhythm of alternating retraction and protraction; similar responses were obtained in response to tactile stimulation (Fig. 2, tracing (a)). The dorsal roots (VIII-XI) of the right posterior limb were then severed and the same type of stimulation reapplied; in this case, all traces of a rhythmical response disappeared and could not be elicited by altering the duration or intensity of the stimulus; the right hindlimb invariably responded monophasically by retraction and remained in this position during the remainder of the stimulation and afterwards.

Precisely similar experiments were performed with an intact forelimb—the other three being de-efferentated. Here, again, a stimulus applied in the form of a series of gentle taps to any of the three de-efferentated limbs elicited a rhythm of movements in an intact right forelimb (Fig. 3, tracing (a)). As soon as the sensory roots (III and IV) of the intact limb were cut, all trace of rhythmical response ceased and was replaced by a monophasic response whose nature is described in the next section.

As is well known, Graham Brown (1912*a, b*; 1913) induced rhythmical movements in de-afferentated mammalian muscles by bilateral stimulation of sensory nerves. We have repeatedly attempted to induce stepping in the limbs of a toad by similar means. We have, however, been completely unsuccessful, although we have not infrequently observed biphasic movements in a limb by periodic variation in the intensity of persistent stimulation applied to the cut end of its own dorsal roots or those of the contralateral limb. The nature of these responses varies very greatly with the nature and intensity of the stimulus and it is premature to assume that they have any ambulatory significance.

C. THE MONOPHASIC RESPONSES OF LIMBS ISOLATED FROM ALL PROPRIOCEPTOR STIMULATION

As stated above, the response of a de-afferentated limb to tactile stimulation applied to the body or to one of the remaining limbs is invariably monophasic provided that the body and remaining limbs are de-efferentated. No proprioceptor activity can be displayed by such a preparation; the de-afferentated limb provides a motor field of response to the extensive sensory area provided by the body and remaining limbs.

(Legend for Fig. 1)

Fig. 1. Records showing the response of a right posterior limb of a toad (a) before, and (b-e) after its de-afferentation. Stimulation was applied to the de-efferentated left posterior limb; all other spinal nerves were cut. (a) Response to electrical stimulation (condenser discharges) of the left plantar surface. Note the rhythmic response. (d) After de-afferentation of the right posterior limb a similar stimulus produces a monophasic retraction (crossed extensor). Tactile stimulation, either short or prolonged (b, c, e 2), produces the same monophasic response, as does electrical stimulation of the dorsal roots of the left hindlimb (e 1).

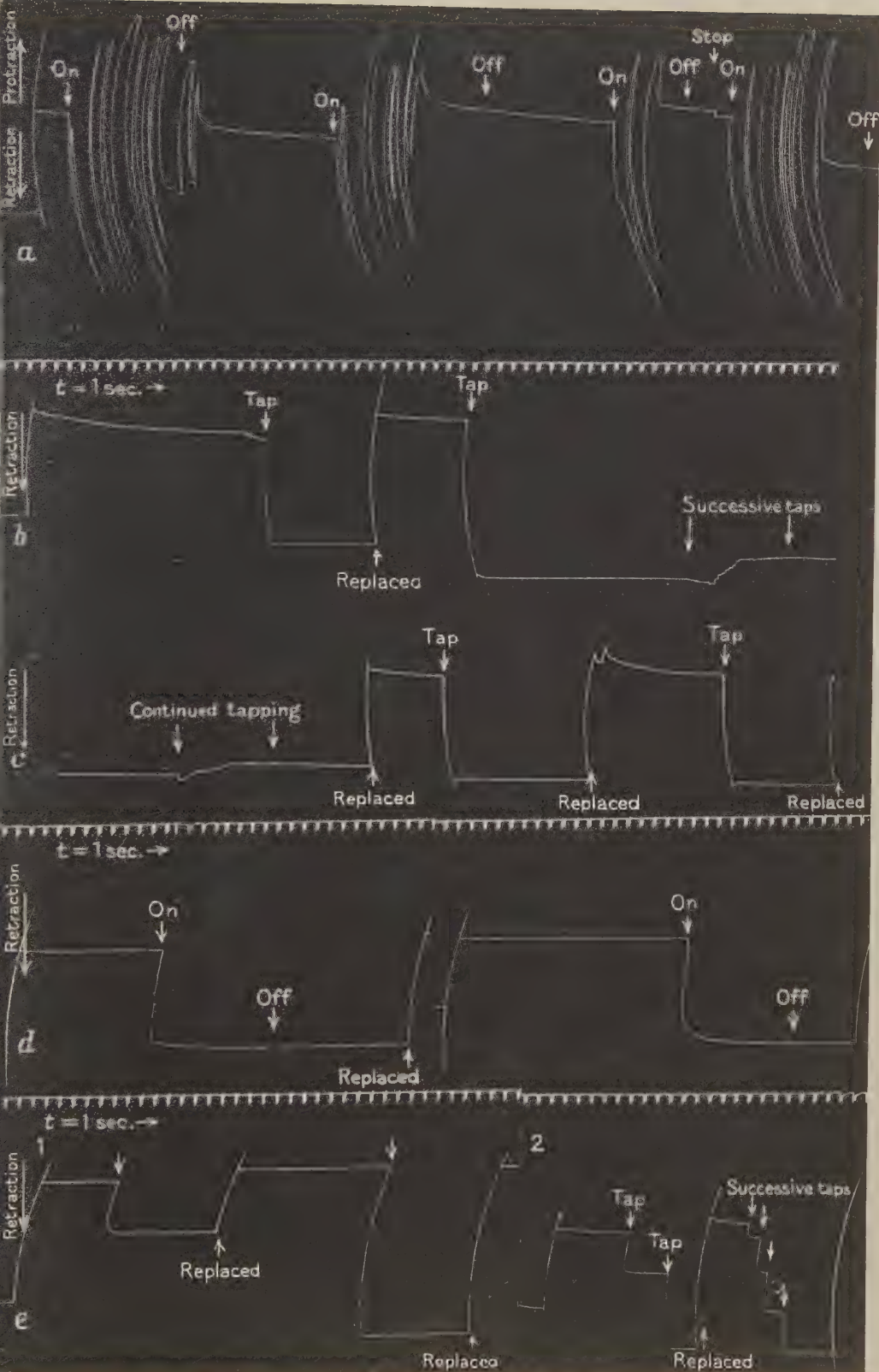


Fig. 1.

The reflex behaviour of such preparations is extremely constant and has been examined in some detail. If the right forelimb is de-afferented and the other three

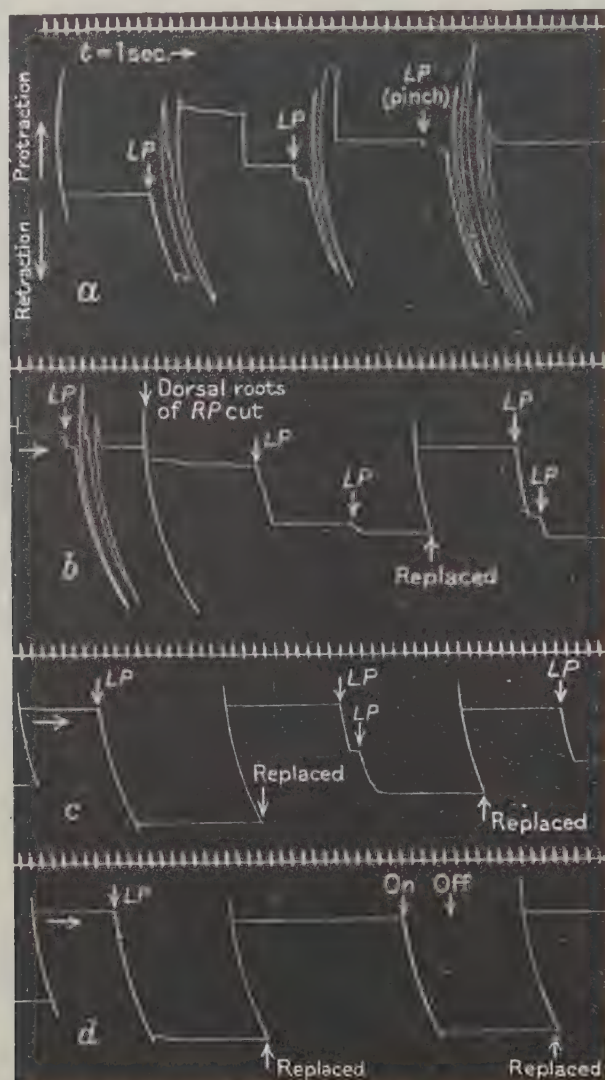


Fig. 2. Records showing the response of a right posterior limb of a toad before and after de-afferentation. Stimulation was applied to the de-afferented left posterior limb. Forelimbs and body were denervated. (a) Rhythmic response of the intact limb after mechanical stimulation. (b) and (c) Identical stimulation elicits a monophasic extensor reaction after the dorsal roots of the right posterior limb are severed. (d) Electrical stimulation of the dorsal roots of the left hindleg produces similar monophasic reactions.

de-afferented, the reflex picture is as follows: starting with the right forelimb passively flexed at the elbow (Fig. 4a1), a gentle tap applied to the right hindlimb causes the right forelimb to be extended laterally from the body and to pronate (Fig. 4a2); similar stimulation of the left hindlimb at once causes the right forelimb to

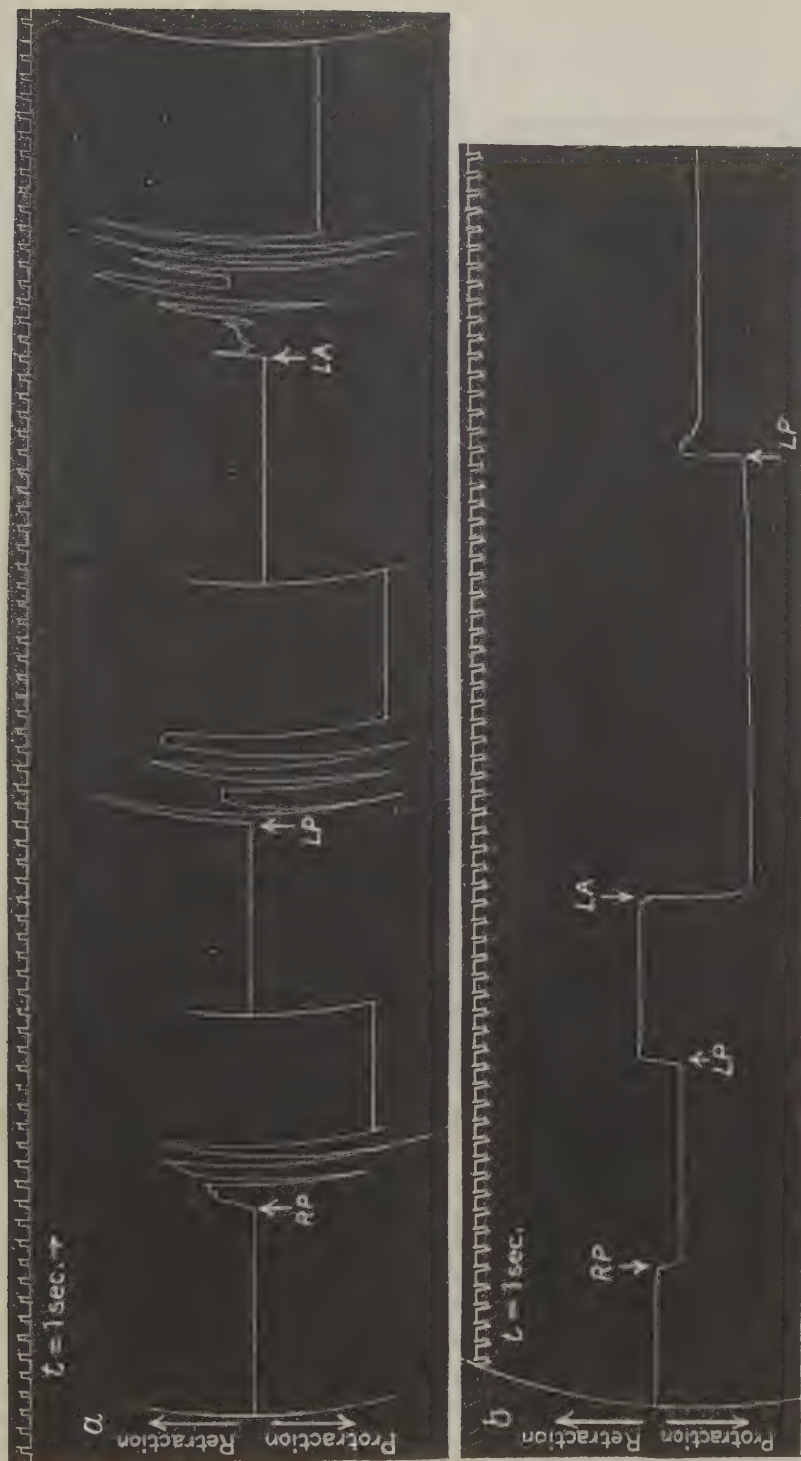


Fig. 3. Records showing the response of the right anterior limb of a toad before and after its own dorsal roots are severed. Stimulation was applied to the three remaining limbs, which were de-afferented. The body was denervated. (a) Rhythmic responses before de-afferentation of the right anterior limb. (b) Monophasic responses after de-afferentation.

retract (Fig. 4a 3), whilst stimulation of the left forelimb causes the right forelimb to return to its original flexed position with the foot near the median line (Fig. 4a 4). It will be noted that all these monophasic responses are of such a nature as, under normal circumstances, would tend to move the animal away from the source of stimulation.

Precisely comparable responses are obtained from a de-afferentated hindlimb; in Fig. 4b the right hindlimb was de-afferentated whilst the motor roots were cut and the sensory roots left intact in the remaining three limbs. If the right forelimb is then stimulated the right femur is partially retracted whilst the knee remains extended (Fig. 4b 2), thus displacing the foot laterally to the right. If a sharp tap be applied to the left hindlimb or if this limb be seized by forceps, the right hindlimb sharply extends (Fig. 4b 3); this is the well-known *crossed extensor reflex*; if now the left forelimb be similarly stimulated, the right hindlimb at once flexes (*diagonal flexor reflex*) (Fig. 4b 4). Again, the response of each of the three limbs is such as would, if the plantar surface remained stationary relative to the ground, co-operate in a movement of the body away from the site of the stimulus.

By combining the appropriate phase of Figs 4a and b, it is possible to reconstruct the simultaneous reactions of the right hind-, right fore- and left forelimbs in response to a stimulus applied to the left hindlimb, viz. the right hindlimb would extend (Fig. 4b 3), the left forelimb would be abducted and extended laterally (mirror image of Fig. 4a 2), and the right forelimb would be retracted (Fig. 4a 3). The body would be moved anteriorly and swung towards the right side, i.e. in a direction away from the stimulus which was applied posteriorly over the left side. In an exactly similar way a stimulus applied to a de-efferentated left forelimb would induce flexion of the right hindlimb (Fig. 4b 4), abduction of the left hindlimb (mirror image of Fig. 4b 2), and adduction of the right forelimb (Fig. 4a 4); the right fore- and left hindlimbs would co-operate to move the body to the right side away from the stimulus. This picture has been checked experimentally by using a de-efferentated left forelimb as the sensory field and the remaining three de-afferentated limbs as the motor field. A preparation of this type is shown in Fig. 4c; on stimulating the left forelimb, the right forelimb adducts, the right hindlimb flexes, and the left hindlimb extends. The only difference between this figure and the reconstructed pattern from Figs. 4a and b is the retraction of the thigh and extension of the ankle of the left hindlimb in Fig. 4c; in this case the body would move forward as well as to the right side.

It should be noted that in all the responses described in this section, the posture adopted by a limb in response to tactile stimulation is independent of its original posture before stimulation. In every case the response is monophasic and the complete absence of rhythmical ambulatory movements confirms our belief that the walking rhythm induced in an intact animal by tactile stimulation involves proprioceptor reflexes which arise either within the limbs themselves or within the muscles of the body. If tactile stimulation excites any intrinsic ambulatory rhythmicity within the central nervous system the latter is quite unable to express itself unless reinforced by stimuli of proprioceptor origin. On the other hand, the response of de-afferentated musculature to tactile stimulation is clearly of functional

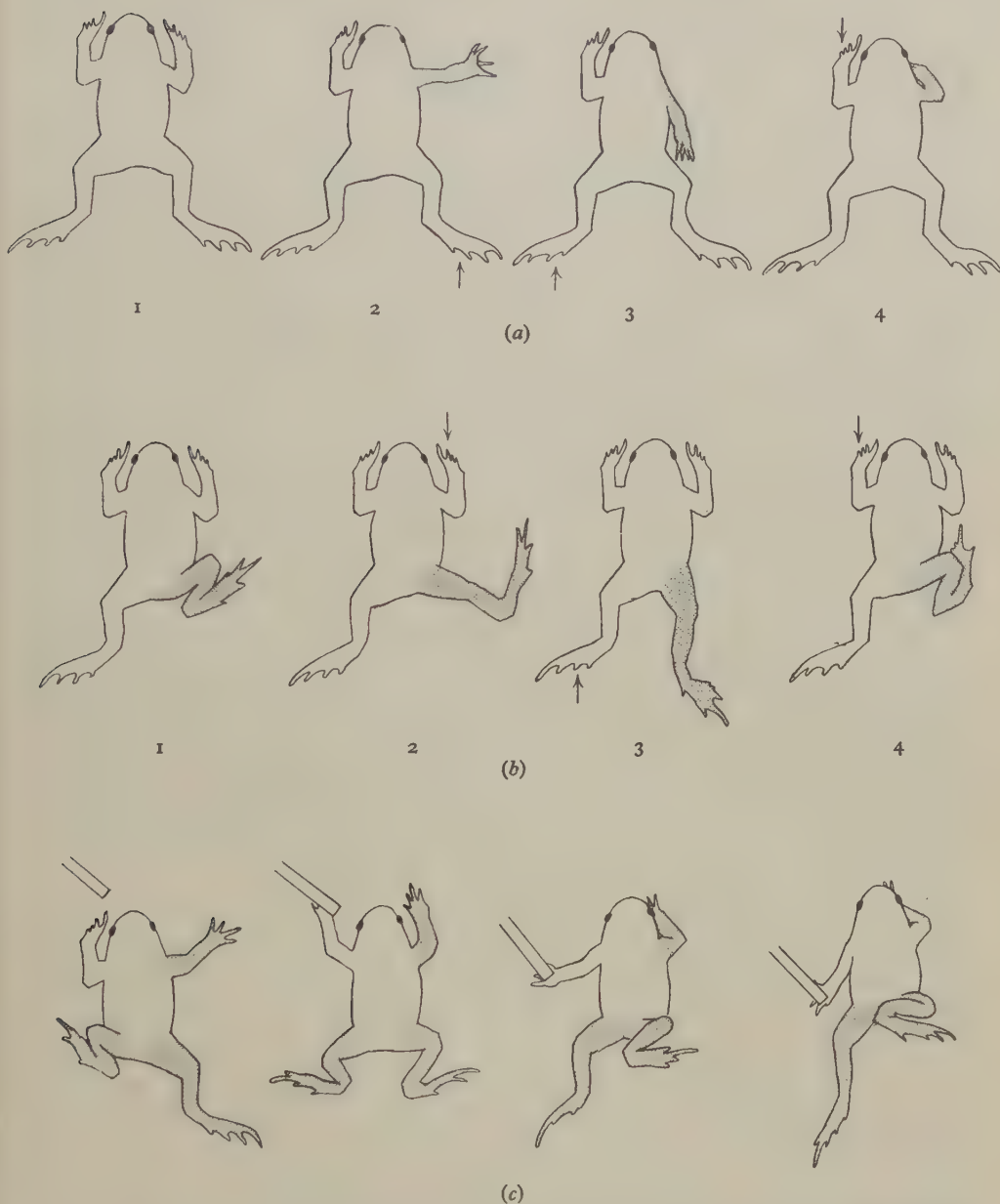


Fig. 4. Reflex postures of de-afferentated limbs. The shaded areas represent regions in which only the motor nerves are left intact, the white areas correspond to regions with only the sensory nerves intact. The arrows indicate the sites of stimulation. (a) Monophasic responses of the de-afferentated forelimb. (b) Monophasic responses of the de-afferentated hindlimb. (c) Monophasic responses of three de-afferentated limbs to pressure and passive retraction applied to a left, de-efferentated forelimb. The left figure in each series indicates the passive posture of the limbs before any stimulus was applied.

significance, displaying itself in an intact animal when the strength of an applied tactile stimulus is such as to elicit a response sufficiently powerful to mask the effect of proprioceptor controls.

DISCUSSION

The experiments described above provide strong evidence in support of the view that the co-ordinated limb movements which are characteristic of ambulation in the toad are dependent on the integrity of the sensory and motor elements of at least one spinal nerve. Two somewhat remarkable facts emerge. First, the ability to display normal ambulation varies with the number of segments possessing an intact nerve supply and not on the position of these segments. Secondly, the extent of the muscular field, over which the sensory equipment of a single spinal nerve can exert its influence, is surprisingly wide. As already stated, an intact XIth dorsal root on one side of the body can sustain a reasonable number of well co-ordinated steps; this nerve supplies only a very limited region of the body in the neighbourhood of the anus and according to Birge (1882) contains, in the case of the frog, only forty-one sensory fibres. As shown elsewhere (Gray, 1944), there are few if any of the somatic muscles which are not involved in the process of ambulation, but, nevertheless, it is remarkable that impulses arising in a very small fragment of the total musculature should be sufficient to control the activity of the whole. The effect of de-afferentation in the toad seems somewhat analogous to the effect of decortication in mammals where the amount rather than the site of the operation is the controlling factor. At the same time, the observations described in this paper show that a localized exteroceptive stimulus may spread over just as wide a field of de-afferentated musculature as that which participates in the ambulation of an animal whose proprioceptor endings are confined to one segment of the body. Experimental evidence of the wide muscular field which responds to a localized proprioceptor stimulus will be given in a subsequent paper.

Although the integrity of one segment of the peripheral nervous system is decisive for the maintenance of an ambulatory rhythm it must not be assumed that all rhythmical limb movements are dependent on the activity of the proprioceptor mechanism. As reported in our previous paper, de-afferentation of all the spinal nerves does not abolish the swimming rhythm in the toad. For reasons to be given later, it does not follow that the swimming rhythm is therefore of central origin, and it is not surprising that it should persist under circumstances which cannot support ambulation: an intact toad invariably swims when, by immersion in water, its limbs and body are deprived of exteroceptive stimulation: walking only occurs when contact with the ground is established by regions of the body whose sensory equipment is intact. We have had numerous instances of animals with four limbs and body de-afferentated performing well-defined synchronous swimming movements with their hindlegs when both body and limbs were in contact with the ground. As will be shown elsewhere, these movements are dependent on the presence of the membranous labyrinth; labyrinthectomy and de-afferentation together totally abolish all swimming movements.

In describing the decrease of spontaneity and smoothness of the ambulatory pattern which attends extensive de-afferentation in amphibia, Weiss (1941*b*, p. 71) states that 'neither of which defects, however, can obscure the fact that the typical co-ordination patterns of levels *O* and *S*, the former integrating muscles into limb movements and the latter integrating different limbs among one another, have not been abolished and cannot therefore be under sensory guidance'. We find it impossible to harmonize this conclusion with the experimental data. In his original paper, Weiss (1936) restricted his account of extensive de-afferentation in the toad to two animals—in one of which some of the dorsal roots of the vertebral segments remained intact; the only direct reference to the ambulatory activity of these two animals was that the animals moved occasionally 'for a few steps with the hind legs alternating as in walking'; otherwise the animals displayed 'a change from normal which was immensely greater than one would expect from simply adding up the effects of forelimb and hindlimb de-afferentation' (Weiss, 1936, p. 469) and this locomotory activity was 'extremely poor'. In our experience, this description applies quite satisfactorily to animals in which de-afferentation is not strictly complete in the sense that one at least of the spinal roots remains intact. Throughout his discussion Weiss (1941*b*) attributes considerable significance to the co-ordinated movements displayed by supernumerary limbs which have been grafted on to the body of the Axolotl. We hesitate to assess the precise significance of such movements, but would point out that it is difficult to interpret such movements in a way which differs essentially from that applicable to the movement of a de-afferentated limb; so long as one or more of the normal limbs possess an intact sensory and motor nerve supply, the supernumerary limb is free to receive reflex stimulation from peripheral sense organs as well as patterns of impulses from an inherently central source. Until the supernumerary limb can be shown to function normally in the absence of such peripheral sources of excitation, positive evidence for the existence of a central type of control must remain lacking. It must be remembered that, during ambulation, the limbs of an animal can only function satisfactorily if the muscles are free to alter in length. Isometric contraction and locomotion are mutually exclusive. If the central nervous system plays a predetermined 'score' (Weiss) the resultant muscular pattern can have no functional significance unless the environment is such as to allow the muscle to undergo an appropriate change in length.

As previously mentioned (Gray & Lissmann, 1940), the behaviour of a de-afferentated mammalian limb is somewhat different from that of an amphibian; recent work suggests, however, that there are, at least, certain features in common. Smith, Mettler & Cuiller (1940) have succeeded in eliciting a phasic response in the intact forelimb of the cat by bipolar stimulation of the cerebral cortex; after cutting the dorsal roots of the limb, however, the response became monophasic and the limb was sustained in full flexion. In a later paper, Mettler & Mettler (1940) reported that so long as three limbs of a cat were intact and available for locomotion, the fourth limb, if de-afferentated, exhibited phasic movements superimposed on a semiflexed posture—the movements corresponding in a general way with the

locomotory pattern. They concluded that normal phasic movement is essentially due to an ability on the part of kinaesthetic impulses to alter the balance of the 'spinal discharge reserve' now in one direction and now in another. Our observations on the toad bring us into substantial agreement with this conclusion.

SUMMARY

1. An examination of a large number of toads has confirmed the conclusion that unilateral integrity of the sensory and motor nerve supply to one segment is necessary for the maintenance of the normal diagonal pattern of ambulation. The site of the intact segment is immaterial; segments of the body are equally effective as those of a limb provided the number of sensory nerve fibres is approximately the same.

2. If three limbs and the body are de-afferentated, a stimulus applied to the fourth intact limb can evoke well co-ordinated ambulation in all four limbs. If the motor roots of the fourth limb are cut, a stimulus applied to this limb invariably elicits only a monophasic response in each of the remaining three limbs. The nature of the monophasic response is always such as tends to move the body away from the source of stimulation.

3. A central nervous system totally isolated from stimulation of proprioceptor or labyrinthine origin cannot sustain co-ordinated movements of a toad either on land or in water.

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THE CO-ORDINATION OF LIMB MOVEMENTS IN THE AMPHIBIA

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(With Six Text-figures)

PROPRIOCEPTOR RESPONSES IN THE LIMBS OF AMPHIBIA

In a previous paper (Gray & Lissmann, 1946) we have shown that a toad can display a normal diagonal rhythm of limb movements so long as the musculature of one spinal segment of the body retains its sensory and motor nerve supply, all other sensory spinal nerves being cut; if the motor nerves to the intact segment are then severed all ambulatory responses cease. It is, therefore, of interest to consider by experimental means how far activity within the muscles or joints of one segment can elicit co-ordinated muscular response over the whole field of the animal's ambulatory musculature. The present paper records observations relevant to this suggestion. It is very much easier to excite controllable proprioceptor activity in a limb than in the vertebral segments of the body, and much easier to record the muscular response of a limb than that of a vertebral segment; consequently, the following analysis is restricted to a study of the extent of the field of response to proprioceptive activity set up in a single limb. Roughly speaking the proprioceptive activity is of two types: (i) that which arises when the retractor musculature of a limb is compelled to contract against an external resistance, (ii) that which arises when a muscle or group of muscles is subjected to passive stretch.

A. RESPONSE OF THE AMBULATORY MUSCULATURE TO EXTERNAL RESISTANCES ACTING AGAINST THE PLANTAR SURFACE OF A LIMB

A normal intact animal whose limbs and body are completely out of contact with objects capable of exerting forces against the retractor muscles of its limbs never exhibits ambulatory movements; when subjected to an extraneous stimulus such an animal swims. On the other hand, an animal whose feet are exposed to quite a low level of extraneous stimulation from a rigid surface invariably exhibits typical diagonal ambulation; it never swims. An object attached to the plantar surface and free to move with the foot itself does not induce ambulation; it is essential that the object should exercise a critical resistance to the limb movement and that this should be concentrated towards the distal end of the limb and not, as in swimming, be distributed over its whole surface. The magnitude of the resistances acting at the feet may be extremely small; it can be visualized by placing a small toad on the

surface of mercury which is covered by a thin layer of water, the depth of which is adjusted until the animal swims readily when out of contact with the walls of the container. If, now, a few glass beads are placed on the surface of the mercury the swimming rhythm is immediately replaced by an ambulatory rhythm although both feet and glass beads slip freely on the surface of the mercury. A fundamental requirement for ambulation is, under normal conditions, the ability of at least one limb to exercise a pull against a relatively rigid object.

In order to observe and record the response of the ambulatory musculature to the type of proprioceptor activity set up when the muscles of one limb are compelled to contract against an external restraint, it has been found convenient to attach rigid clips to the iliac bones. Preparations of this type can be suspended in air or in water with their plantar surfaces either in or out of contact with a horizontal sheet of glass.

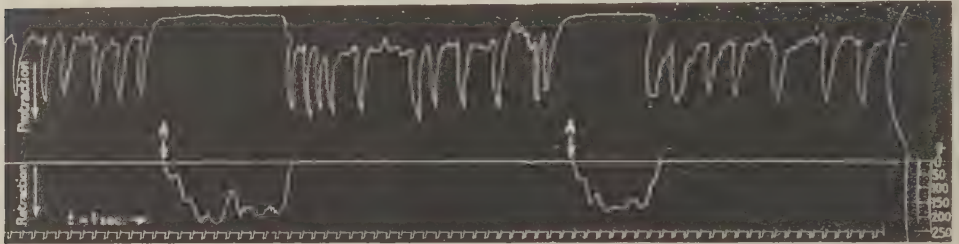


Fig. 1. Record showing the retractor-extensor thrust in an intact left posterior limb. A normal toad was suspended by means of threads with its feet in contact with a glass plate, over which the plantar surfaces could slip freely and thus exhibit typical diagonal ambulation. The ambulatory movements of the *LH* limb are shown isototonically in the upper tracing. Whenever the limb was allowed to press against an isometric lever, when approaching the later phase of a retraction (signals *A, A* on lower tracing), the ambulatory rhythm ceased and the limb exerted a sustained but variable pressure against the lever. As soon as the lever was removed, ambulatory movements were resumed.

Provided the feet are in contact with the glass, a gentle stimulus applied to one limb elicits normal ambulatory movements in all four limbs. If, when all four limbs are stepping freely in diagonal sequence, one of the limbs (*A*) be allowed to come into contact with an isometric lever at a moment when the limb is approaching the end of a propulsive (retractor-extensor) phase of movement, all rhythmical movements in this limb cease; the limb remains at rest exerting a sustained but variable pressure (*retractor-extensor thrust*)* against the lever (Fig. 1). Meanwhile the other three limbs continue their normal rhythmical movements. As soon as limb *A* is released from contact with the lever, flexion ensues and the limb resumes its rhythmical movements in correct phase relationship with the other three limbs.

The power of a limb to exert a sustained retractor-extensor thrust against an external resistance depends entirely on the integrity of the limb's own sensory nerve supply. When the above experiment is repeated with a de-afferented limb, contact

* The term 'retractor-extensor thrust' is used descriptively and is not meant to indicate any close relationship to the 'extensor thrust reflex' of other authors,

with an extraneous resistance does not abolish its rhythmical movements; these continue with the same frequency as that of the movements being executed by the other limbs (Fig. 2). It is clear that a retractor-extensor thrust exists in the toad and that its mechanism is essentially the same as the support reaction in mammals. It is of proprioceptor origin and is profoundly depressed by spinal transection. Except in respect to the last characteristic it is essentially similar to the resistance pull exhibited by fish such as the eel (Gray, 1936).

A retractor-extensor thrust developed by a forelimb in response to external restraint, evokes a marked synergic extensor response in the contralateral hindlimb

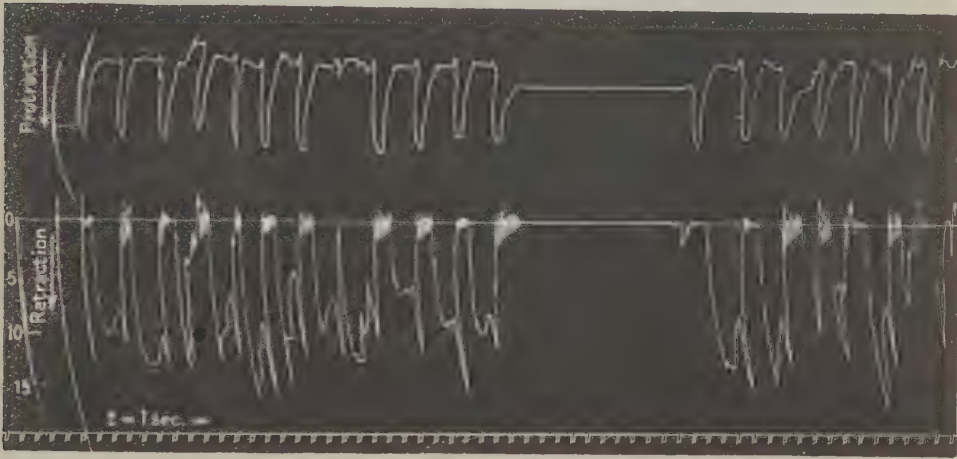
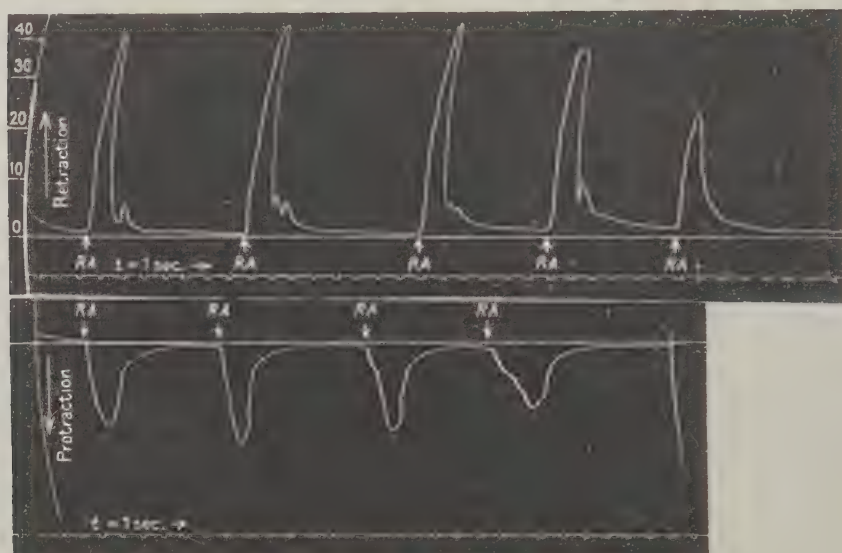


Fig. 2. Record showing the absence of a retractor-extensor thrust in a de-afferented left posterior limb. The upper tracing is from an isotonic lever, and shows that rhythmical movements continue in the limb although the latter is in contact with an isometric lever during the later phases of retraction. The lower tracing from the isometric lever shows the absence of any sustained retractor-extensor thrust.

(*diagonal extensor response*, R_2 , L_2 , Fig. 6). This phenomenon reveals itself with regularity when the hindlimb is de-afferented and thereby released from influences exerted on it from other sources of excitation. The synergic response of a de-afferented left hindlimb is illustrated in the upper tracing in Fig. 3. It should be noted that the synergic thrust from the diagonal limb is of functional significance, since in its absence the body must be exposed to a yawing couple tending to slew it round to one side (Gray, 1944); the synergic action of diagonal limbs during normal ambulation is demonstrated by the direct measurements of Barclay (1946).

Just as a retractor-extensor thrust of one forelimb induces synergic action in the de-afferented diagonal hindlimb, so it induces a protractor response (*crossed anterior protractor response*, R_1 , L_1 , Fig. 6) in the contralateral de-afferented forelimb (Fig. 4). This response is particularly clear if the intact forelimb is allowed to exert its retractor pull whilst in a partially retracted posture. If the intact forelimb exerts its pull whilst in a fully protracted posture, the contralateral forelimb usually

retracts. Both of these responses form part of the co-ordinating mechanism of normal ambulation.



Diagonal extensor and diagonal flexor reflex

Fig. 3. Isometric record showing in the upper tracing the response of a de-afferented left hindlimb to a retractor-extensor thrust developed in a right forelimb; at the signal *RA*, the right forelimb was allowed to engage during retraction with a suitable resistance—the left hindlimb immediately retracted. The lower tracing shows the diagonal flexor response to a pinch (at signals *RA*) applied to the right anterior limb.

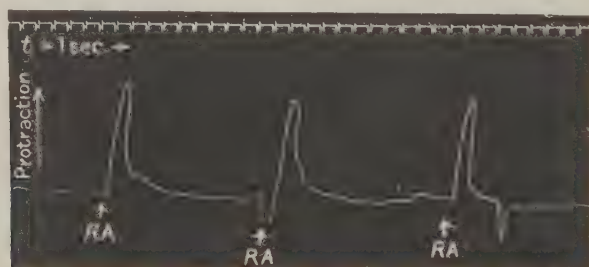


Fig. 4. Isometric record showing the protractor response of a de-afferented contralateral (left) forelimb to a retractor-extensor thrust developed in the other forelimb. At the arrows (*RA*) an intact right forelimb engaged against a resistance.

On mechanical grounds, a retractor-extensor thrust in a forelimb might be expected to induce a protractor-flexor response in a de-afferented ipsilateral hindlimb. Experimental data show that whilst such a limb is in fact protracted, the movement is nevertheless restricted to the femur; the knee, however, remains extended and the whole limb moves forward in an extended posture. How far this

response is to be regarded as part of the normal *placing reaction* (R_3 , L_3 , Fig. 6) is uncertain. If an intact toad is held horizontally in such a way that the two limbs on one side of the body are out of contact with the ground, the two unsupported limbs may either exhibit somewhat irregular movements or remain at rest; if a support is now provided for the forelimb and this limb be allowed to retract, the ipsilateral hindlimb is immediately brought into the protracted flexed position and remains there. As soon as the support for the forelimb is withdrawn the flexed posture of the hindlimb is lost. It is difficult to say how far this placing reaction is of exteroceptive and how far of proprioceptive origin, but it can be elicited with great regularity provided that the axis of the body is approximately horizontal. If the hindquarters of the body are considerably lower than the head, the response is different, and recalls very strikingly the response of the de-afferented limb to a

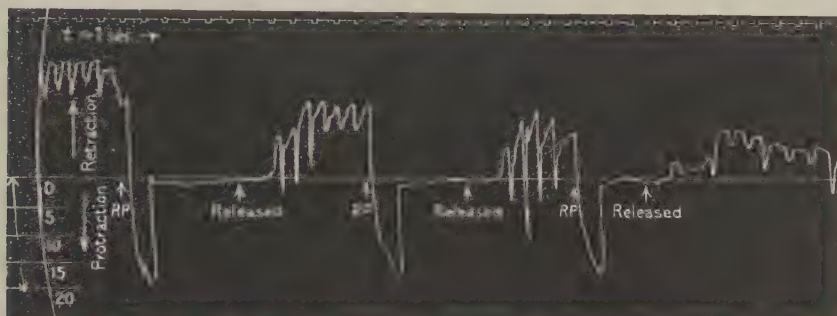


Fig. 5. Isometric record showing the flexor response of a de-afferented left hindlimb to a retractor-extensor thrust developed by the intact contralateral (right) hindlimb. The record begins when the animal was exhibiting swimming movements; at the signal *RP*, the right hindlimb engaged against a resistance—note the protraction of the left hindlimb. When the right hindlimb was released swimming movements were resumed by both limbs.

retractor-extensor thrust in the ipsilateral forelimb. The normal placing reaction of the intact limb seems comparable to that described by Bard (1933) in the cat.

Whereas a retractor-extensor thrust in a forelimb elicits a clearly defined synergic response in a de-afferented diagonal hindlimb, we have not, with equal regularity, observed the converse phenomenon. The most distinctive feature of a thrust developed by a hindlimb is an accompanying flexion in the contralateral hindlimb (*crossed flexor response*; RH_1 , Fig. 6). This phenomenon displays itself when the contralateral hindlimb is de-afferented and when the intact hindlimb, stepping on a glass plate, is allowed to develop a retractor-extensor thrust against an external resistance. A particularly clear case is illustrated in Fig. 5. In this instance the animal was initially suspended freely in air, and both hindlimbs were executing swimming movements; as soon as the intact right hindlimb exerted its retractor-extensor thrust, all swimming movements ceased in both limbs and the de-afferented left posterior limb flexed strongly. It is clear that the two limbs respond in such a way that the body is not exposed to any uncompensated couple tending to make it pitch about its transverse horizontal axis.

The full functional significance of the above facts will be discussed later, but for the moment emphasis may be laid on the extent to which the experimental data indicate the wide extent of ambulatory musculature which is affected by the proprioceptor excitation which arises when a localized region of this musculature contracts against an external resistance. Although it is not strictly relevant to the present inquiry, it may be noted that the response of a wide field of ambulatory musculature to a localized stimulus also occurs when the stimulus is exteroceptive. The lower tracing in Fig. 3 illustrates the flexion of a de-afferentated left posterior limb in response to a pinch applied to the intact right anterior limb; at the same time the right posterior limb extends. All these facts confirm the conclusion that localized stimuli applied to one relatively small part of the whole sensory field elicit a response from a very large part, if not indeed the whole, of the ambulatory musculature.

B. MUSCULAR RESPONSE TO PASSIVE STRETCH

The responses so far considered have all been dependent on the active contraction of an intact limb against an external resistance. In addition, the limbs of a toad exhibit well-defined responses when their inactive musculature is subjected to passive stretch. In the intact animal these proprioceptor responses are usually masked by others of labyrinthine origin, and it is therefore necessary to remove both labyrinths in order to display the proprioceptor responses in their most obvious form. If the hindquarters of such a preparation be supported by the hand whilst the forelimbs remain on the ground, the animal remains motionless, but if the hindquarters are now pushed gently forwards, thus passively retracting the forelimbs, the latter step forwards regularly and alternately; if the hindquarters are drawn backwards, the forelimbs step backwards; if the hindquarters are displaced to the right, the forelimb steps towards the right by active abduction of the right forelimb and adduction of the left forelimb. Precisely similar phenomena are displayed by the hindlimbs if the forequarters of the body are supported; if the hindlimbs are placed one on each side of the centre of rotation of a turn-table, one limb will step forwards whilst the other steps backwards. Thus for a very wide range of passive muscular stretch the limbs respond in such a way as to reduce the length of the stretched muscles. It should be noted that the response is not necessarily restricted to the stretched muscles. The forward step which occurs in response to the stretch of the protractor musculature involves all the muscles concerned with the normal protractor phase of progression; the limb is lifted from the ground, swung forwards and replaced on the ground. The muscles involved in the response to stretch of the retractor muscles are, however, not the same as in the retractor phase of progression; the limb is lifted from the ground whilst being retracted—whereas when walking the limb remains on the ground during the retractor phase.

The influence of a passive stretch applied to one limb on the behaviour of the other limbs of a spinal toad has already been described in a previous paper (Gray & Lissmann, 1940). It is, however, best illustrated by preparations in which one forelimb is left intact whilst the other three are de-afferentated. When such a preparation is at rest with the intact right forelimb protracted, the right hindlimb can

be placed passively in a state of full flexion and the left hindlimb in full extension. If the right forelimb is now passively retracted it responds by protraction and flexion, but at the same time the right hindlimb extends (*ipsilateral extensor response*; R_4 , L_4 , Fig. 6) and the left hindlimb flexes (*diagonal flexor response*; R_5 , L_5 , Fig. 6). These responses are figured elsewhere (Gray, 1940). It will be noted that so far as the diagonal hindlimb is concerned the response to passive retraction of a forelimb is the exact opposite to that elicited by the pull of the forelimb against an external resistance.

C. FUNCTIONAL SIGNIFICANCE OF PROPRIOCEPTOR RESPONSES

The possibility of integrating the various proprioceptor reflexes into one functional unit can best be visualized by observation of an intact toad freely immersed in water. Such an animal rests with both forelimbs protracted and both hindlimbs retracted, and the locomotory pattern which can be elicited from it depends entirely on the presence or absence of mechanical forces operating against the feet. The animal invariably swims if these forces are absent, it invariably walks if they are present, and the transition from one form of progression to the other can readily be controlled by providing or withdrawing a *point d'appui* for the feet.

The transition from swimming to walking takes place with extreme smoothness and is not easy to follow by the naked eye; the following account is based on cinematograph records of animals landing on a relatively level surface. During active swimming both forelimbs are closely adducted to the sides of the body, and contact with the landing stage is first established by the ventral surface of head and throat; both forelimbs are then immediately protracted (Fig. 6, phase I). As soon as one of these limbs (e.g. the left, as in Fig. 6) establishes and maintains contact with the ground a definite response is exhibited by each of the other three limbs. The contralateral hindlimb retracts and extends, the ipsilateral right hindlimb protracts and flexes, and the right forelimb protracts. In this way phase II of Fig. 6 is reached; these postures are impressed on the limbs irrespective of the phase of swimming movement which may exist at the moment that the left forelimb exerts its pull on the ground. The protraction of the right forelimb is essentially an expression of the *crossed anterior protractor response* (L_1 , Fig. 6; see also p. 135), and the retraction of the contralateral right hindlimb is the *diagonal extensor response* (L_2 , Fig. 6; see also p. 135). The protraction of the left hindlimb (L_3) is the normal *ipsilateral placing reaction* (see p. 137). On reaching the posture shown in phase II, Fig. 6, the right forelimb in turn establishes effective contact with the ground and thereby elicits (R_{1-3}), the posture shown in phase III, Fig. 6. It may, however, be noted that in the case of the two hindlimbs the responses (R_2 , R_3) elicited by the right forelimb are reinforced by the *ipsilateral extensor* (L_4) and *diagonal flexor* (L_5) responses to the protraction of the left forelimb. At phase III the left forelimb establishes contact with the ground for the second time, and since the right hindlimb is now on the ground the ensuing flexion of the left hindlimb receives additional reinforcement from the *crossed flexor response* (RH_1 , Fig. 6). In passing from phase III to phase IV the reflex pattern involved includes L_{1-3} , due to the retractor-extensor thrust of the

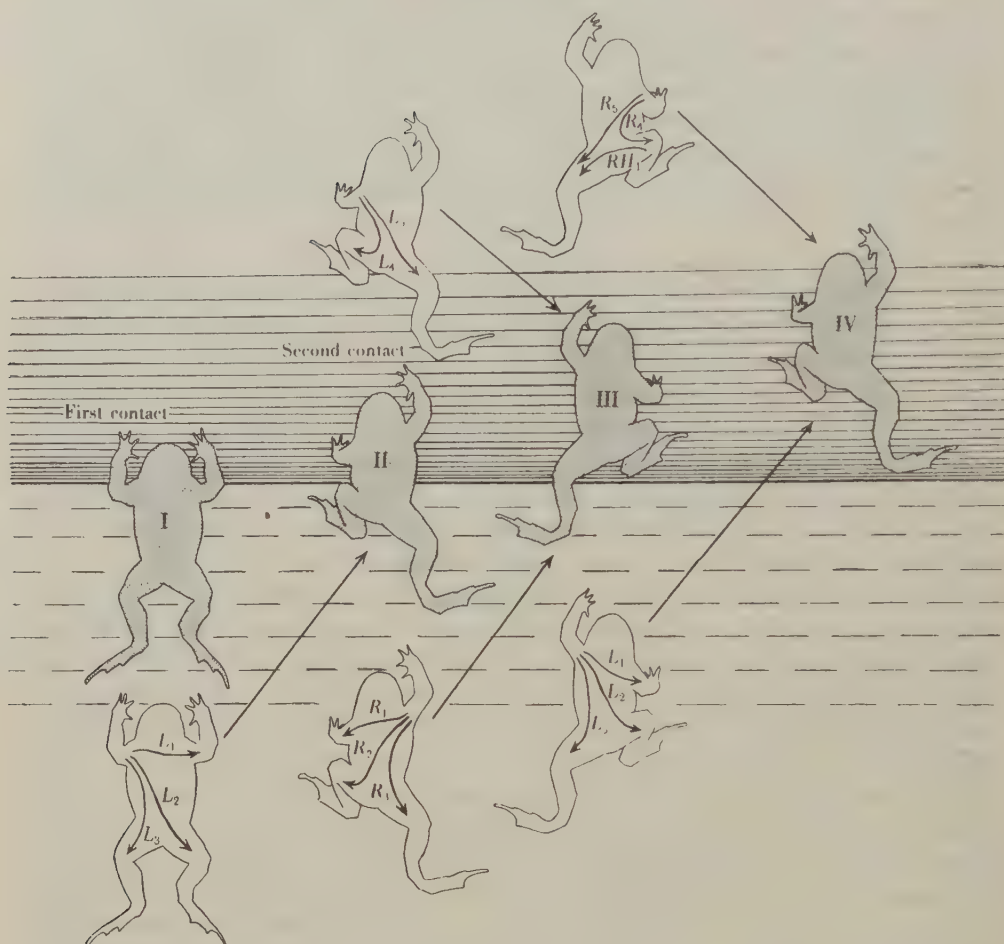


Fig. 6. Diagram illustrating the patterns of reflexes associated with the transition from swimming to walking. The shaded outlines I-IV show successive postures of the limbs when the animal emerges from water to the solid ground indicated in the upper half of the diagram. The unshaded figures show the reflex mechanisms responsible for phases II-IV. In phase I both hindlimbs are flexing simultaneously in normal swimming and both forelimbs are partially protracted. The first effective contact with the ground is established by the left forelimb. The retractor-extensor activity of this limb facilitates a crossed protraction response (L_1) in the right forelimb, a diagonal extensor response (L_2) in the right hindlimb, and an ipsilateral placing response (L_3) in the left hindlimb; these responses yield phase II. At this moment, the right forelimb engages with the ground, thereby inducing corresponding responses (R_{1-3}); at the same time the left forelimb in response to stretch of its protractor muscles swings forward and thus induces retraction of the left hindlimb (L_4 , ipsilateral extensor response) and protraction of the right hindlimb (L_5 , diagonal flexor response); these responses yield phase III. Note that L_4 reinforces R_2 and L_5 reinforces R_3 ; since in phase III the right hindlimb is brought into contact with the ground, subsequent flexion of the left hindlimb in passing from phase III to phase IV is reinforced also by a crossed flexor response (RH_1). $L_{1,3}$ and R_{1-3} , responses due to the fixation of the left and right forefeet respectively. L_1 , R_1 , crossed anterior protractor responses. L_2 , R_2 , diagonal extensor responses. L_3 , R_3 , ipsilateral placing responses. $L_{4,5}$, $R_{4,5}$, responses due to protraction of the left and right forefeet respectively. L_4 , R_4 , ipsilateral extensor responses. L_5 , R_5 , diagonal flexor responses. RH_1 , crossed flexor response due to fixation of right hindfoot.

left forelimb; R_4 and R_5 due to protraction of the right forelimb, and RH_1 due to the retractor-extensor thrust of the right hindlimb. At phase IV the body is carried on an effective triangle of support provided by the right fore- and both hindfeet, the left forefoot being free to protract; from this point onwards normal ambulation proceeds.

From this point of view, the transition from swimming to walking is largely due to the fact that each hindlimb comes under the control of the proprioceptor excitation arising in the forelimbs. It must be remembered, however, that diagonal co-ordination can still be exhibited when both forelimbs have been de-afferented and even after all four limbs are desensitized. The ability of the proprioceptive activity of the forelimbs to 'drive' de-afferented hindlimbs is probably only a special case of the general conclusion that sensory activity in all parts of the whole ambulatory mechanism exerts its effect over the entire muscular field.

D. THE RELATIONSHIP OF THE AMBULATORY RHYTHM TO PROPRIOCEPTOR EXCITATION

Although there is clear evidence that localized patterns of sensory activity can elicit well-defined and widespread muscular co-ordination, it is very important to bear in mind that the behaviour of each individual limb depends in practice on the whole field of sensory activity playing on the motor centres of its musculature. For example, although a forelimb can, by exerting an adequate retractor-extensor thrust, induce synergic extension in a diagonal hindlimb—nevertheless, the hindlimb retains a considerable range of independence in its response to other sources of excitation. In order to clarify the position it is convenient to consider the maintenance of an ambulatory rhythm in a limb which can only be influenced by its own sensory activity. The limb can be regarded as having two motor centres—one concerned with the retractor and extensor muscles and the other with the protractors and flexors; these two centres can be assumed to be incapable of simultaneous activity. Most, if not all, the experimental data can be harmonized with the suggestion that if one of these two centres is to excite its associated musculature it must be exposed to a greater balance of excitatory over inhibitory influences than is the case of the other centre. Starting with a limb at rest in a protracted posture, an extraneous stimulus applied to the retractor centre will cause the limb to retract. The protractor muscles are thereby stretched, and the resultant proprioceptive activity raises the level of excitation of their associated motor centres. The relative excess balance of excitation of the retractor centres is thereby reduced, and eventually the balance of excitation over inhibition moves in favour of the protractor centres; the limb then protracts and the cycle is repeated. If, during its phase of retraction, the limb encounters an external resistance, the excitatory balance of the retractor centres is reinforced by the proprioceptor activity of the retractor-extensor thrust, and the balance is thereby maintained in favour of the retractor centres until such time as the resistance is overcome.

The excitatory balance in one limb is, however, influenced by events occurring in other limbs. Starting with an excitatory balance in favour of the retractor-extensor centre of the right forelimb any proprioceptor activity induced by an

external resistance to this limb produces a stream of impulses tending to swing the excitatory balance of the diagonal left hindlimb in favour of the latter's retractor-extensor centres (*diagonal extensor reflex*). The effect of this stream of impulses to the diagonal limb will depend on the nature of the excitatory balance existing at that moment in the centres of this limb; if the existing balance is only slightly in favour of the protractor centre the balance may be swung to the retractor side, protraction will then cease, and retraction ensue; on the other hand, if the existing balance is in favour of retraction, the effect of the diagonal limb will be to prolong or intensify retraction in the hindlimb; similarly, an extensor thrust developing in one hindlimb in response to an external restraint will, owing to the *crossed flexor reflex*, tend to swing the balance of excitation of the contralateral limb towards the protractor-flexor side and consequently increase the difference in phase of movement of the two hindlimbs. An integration of all these responses appears to yield part of the whole co-ordinated picture of diagonal limb movements which is observed during normal ambulation. It remains to be seen how far the above concepts can be applied to the behaviour of the limbs when the animal is swimming or jumping.

SUMMARY

1. Well-defined myotactic reflexes (retractor-extensor thrusts) can be elicited from the retractor and extensor musculature when these muscles contract against an external resistance. A de-afferentated limb cannot exert a retractor-extensor thrust.
2. A retractor-extensor thrust arising in a forelimb evokes an extensor response in the diagonal hindlimb and a protractor response in the contralateral forelimb. In order that these responses should display themselves with regularity it is necessary to de-afferentate the responding limb; in an intact limb they are often masked by the control exerted by the limb's own proprioceptive mechanism.
3. In an intact animal a retractor-extensor thrust in a forelimb evokes a 'placing reaction' from the ipsilateral hindlimb. This phenomenon is only partially displayed if the hindlimb is de-afferentated.
4. When an intact forelimb responds, by protraction, to passive stretch, the contralateral hindlimb flexes and the ipsilateral hindlimb extends if the latter limbs have been de-afferentated.
5. The individual proprioceptor limb responses integrate to form an adequate picture of the co-ordinated limb movements seen when an intact toad ceases to swim and begins to walk on land.
6. The role of proprioceptor activity in the maintenance of an ambulatory rhythm in a single limb is discussed.

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THE NEUROLOGICAL BASIS OF THE LOCOMOTORY RHYTHM IN THE SPINAL DOGFISH (*SCYLLIUM CANICULA*, *ACANTHIAS VULGARIS*)

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(With Fifteen Text-figures)

INTRODUCTION

One of the crucial problems of animal behaviour concerns the *spontaneity* or *drive* behind the motor activities, another the *pattern* or *co-ordination* of the various phases of movement. In this connexion the study of some elementary motor patterns, such as respiration, locomotion, cleaning and scratching, has led to far-reaching conclusions, which have also been applied to more complex acts of behaviour (Lorenz, 1939).

One theory presents the animal as an intrinsically active system, which only comes to rest under suitable inhibitory stimuli; according to another it is normally at rest, and is only activated by suitable excitatory stimuli. Consequently, if removal of all sources of outside stimulation caused perpetual activity in a preparation, this would support the former theory; if, on the other hand, the preparation was in the first place perpetually active and became silent when all sensory influx was cut off, this would favour the latter. At the same time, the existence side by side of excitatory and inhibitory stimuli adds to the complications.

In recent years, however, the investigation of lower vertebrates—notably by Adrian, von Holst and P. Weiss—has produced a very definite picture based on the conception that rhythmically co-ordinated movements are driven and governed by an automatic mechanism within the central nervous system, and are not essentially dependent on any kind of afferent inflow. Since Adrian & Buytendijk (1931) recorded from the isolated brain stem of the gold fish slow changes of electrical potential which were more or less of the same order of frequency as the opercular movements, it has become customary to regard such changes as the expression of a spontaneous, automatic driving mechanism for various rhythmic activities. Under certain conditions, in fish, the respiratory and locomotory movements become synchronous. From this von Holst (1934, 1936) concluded that the electrical changes as recorded in the brain stem represent a process which is the common central cause of origin for respiratory and locomotory movements alike; in the normal, intact fish their frequencies merely become modified by regulating influences from the periphery.

It has often been suggested that the underlying mechanism consists of certain groups of ganglia in the central nervous system, which owing to their physiological make up, and under the influence of their normal metabolism, continuously produce a stimulating substance or an electrostatic field. This is said to elicit patterns of motor discharges as soon as a critical level of concentration is reached. At that point the stimulating agent is destroyed and the process starts anew.

In so far as the locomotory rhythms of teleost fish are concerned, von Holst (1939), after extensive research on the subject, has reached the following conclusions: groups of neurones arranged along the spinal cord are responsible for the rhythmic activity; they operate automatically as long as the central excitatory state is kept at a certain level, which is constantly maintained by the medulla. Hence, a medullary preparation is persistently active, whereas a spinal fish merely responds to reflex stimulation. This theory of an internal automatic rhythm which governs the locomotory movements of the trunk appears to have been widely accepted for teleosts and elasmobranchs such as the dogfish (Gray & Sand, 1936; le Mare, 1936), except that in teleosts 'the control of rhythmical movements resides in neurones restricted to the brain, whereas in the dogfish cells all the way down the spinal cord are capable of initiating such movements' (le Mare, p. 437). This additional assumption in the case of the dogfish appeared necessary, because it has been known since Steiner (1885) that a spinal dogfish exhibits a persistent locomotory rhythm.

The dogfish therefore seems to be particularly suitable for an investigation of the problems outlined above. The experiments reported here were designed to throw some light on the two alternative theories, viz. whether the locomotory movements are due to a central drive and a central pattern of activity, or whether they can be considered essentially as moving sites of nervous integration, continuously re-excited from within or without the central nervous system, and ruled by co-ordinating patterns of afferent impulses.

METHOD

The experiments were performed on fourteen individuals of *Scyllium* (*Scylliorhinus*) *canicula*, varying between 55 and 70 cm., and ten *Acanthias vulgaris* (*Squalus acanthias*), 48–75 cm. in length. In the first part of this study the influences were examined which affect the swimming rhythm of spinal preparations. By determining the range of response to various isolated types of stimulation, and by correlating their sequence, one may attempt to build up all phases of the swimming rhythm. For this purpose the spinal animals were fixed by two strong vertical pins through the snout, allowing free lateral movement of the trunk. The persistent swimming and the reflex responses were studied by attaching a writing lever to the anterior end of the base of the first dorsal fin, and kymographically recording the movements. The stimulation employed was mostly tactile: touch with a camel-hair brush, a straw, or a blunt seeker, and diffuse touch to the body by lifting and lowering a glass plate. Other stimuli used must be considered as nociceptive, or involving deep pressure receptors; they were produced by means of a needle, a sharp metal clip or clamp, by pressure applied with the fingers, or a sharp pinch with forceps.

THE SPINAL DOGFISH

The behaviour of the spinal dogfish, *Scyllium canicula* and *S. catulus* has been described by Steiner (1885), Bethe (1899), Bauer (1926), ten Cate (1933), ten Cate & ten Cate-Kazejewa (1933), Gray & Sand (1936) and le Mare (1936). A general survey of the observations suggests that the time has not yet come when they can be brought into satisfactory agreement. As the arising controversial points concern the excitatory and inhibitory stimuli which affect the swimming rhythm, they have been subjected to re-examination. However, no extensive analysis of the various reflexes has been attempted in the present paper, and it must be admitted that many questions are left unanswered. Some of the more striking discrepancies in the results of previous authors and the present observations may perhaps find an explanation along the lines suggested through the interesting observations of Bauer (1926), who describes (i) individual variations, (ii) differences arising from the different age of the specimens (cf. Polimanti, 1911), (iii) different behaviour of preparations according to the length of time elapsed since the operation, and (iv) reflex reversal after fatigue (cf. Gray & Sand, 1936). All observations reported below were made within the first 10 days, usually 2–5 days, after the operation.

While there is considerable disagreement about details, and while the general conclusions reached here are the opposite of those reached by other authors, the most important experimental finding in connexion with our problem has been confirmed for *Scyllium*, and has been found to apply equally for *Acanthias vulgaris*, i.e. a spinal animal of either species, mounted for recording as described above, displays uninterrupted swimming movements for a period of at least some days.

When swimming movements are initiated through exteroceptive stimulation in a spinal teleost fish two distinct processes appear to take place, as has been described by Gray (1936) and von Holst (1935*b*): (1) a rapid development of an undulatory posture over the body, and (2) a propagation of the posture along the body. Although it is not quite obvious in an actively swimming dogfish, there is evidence to show that conditions are essentially similar in both the teleost and the dogfish.

Inactive preparations

Before attempting to analyse the factors which govern the swimming movements, i.e. the passage of the undulatory posture over the body of the dogfish, it seems profitable to study in the inactive preparation the initial spreading of the posture. For this purpose animals can be used which are recovering from the anaesthetic, moribund preparations which have ceased to swim, or animals whose swimming movements have been inhibited (see below). A localized stimulus of short duration, applied to almost any part of the surface, causes the body to be thrown into an S-shape, which may persist for a short period before the body returns to its original outstretched position. The amplitude of the excursion, and the duration at which the reflex figure is held, clearly depend on the strength of the stimulus, and the time of application. The reflex posture itself, i.e. the position of the wave on the body, depends entirely on the site of stimulation. Thus if the base of the first dorsal fin

be attached to the recording lever, and the body stimulated laterally at different levels, it will be noted that a touch to the left at the level of either the pectoral or the first dorsal fin will cause a movement towards the right of the median, while if the body is stimulated at the level of either the pelvic or the second dorsal fin the response will be reversed, and the region of the first dorsal fin will move towards the left (Fig. 1). At a point between the first dorsal fin and the pelvic fin no visible reaction will be recorded. It is interesting to note that von Holst (1934) has described a similar reaction in goldfish in which the spinal cord was transected at different levels; a tail reaction towards one side became progressively smaller the more anteriorly the cut was situated. It is not clear, however, from the report whether the stimulus was also applied more anteriorly, or whether the effect is due to the structural difference of the reacting system and the resulting different integration.

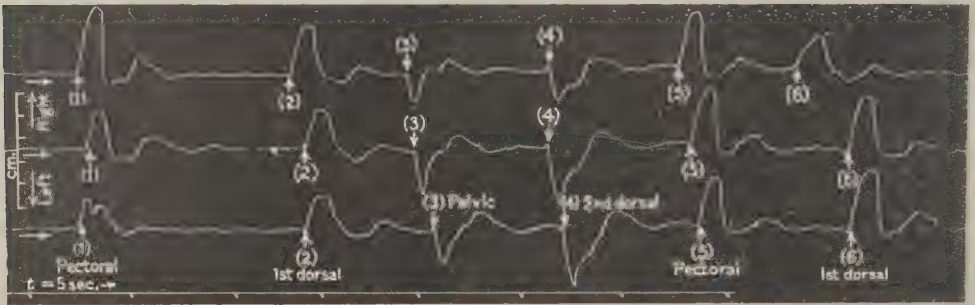


Fig. 1. Response of an inactive spinal preparation of *Acanthias vulgaris* to lateral touch with a camel-hair brush at different levels of the body. The movement of the trunk is recorded from the anterior end of the base of the first dorsal fin. The sequence of stimulation was identical in all three tracings, i.e. to the left at the level of (1) the pectoral, (2) first dorsal, (3) pelvic, (4) second dorsal, (5) pectoral, (6) first dorsal fin. Note that a reversal of the response occurs between the first dorsal and the pelvic fins.

It is also noteworthy that when two opposing stimuli are applied simultaneously, each of which singly causes a monophasic response, no integration or superposition takes place in the sense that they cancel each other out, but the response becomes biphasic, i.e. the movement takes place in both directions in succession (Fig. 2). For instance, if stimulation of the left pectoral fin causes the region of the first dorsal fin to be moved to the right, and stimulation of the right pectoral fin movement to the left, then stimulation of both produces a movement left-right, right-left or left-right-left (Fig. 2*b*). The change from one position to the other is accomplished by a movement of the reflex posture along the body. This type of response recalls similar phenomena in the tetrapod locomotory system, e.g. if the hind leg of a spinal toad be passively extended it responds by flexion; if both legs are simultaneously and passively extended by placing them on to a revolving drum, they flex alternately (Gray & Lissmann, 1940).

Prolonged gentle stimulation (touch with a camel-hair brush or straw) may cause the reflex figure to be held in a tonic contraction, but rarely for more than 5 sec.;

adaptation to the stimulus seems rapid, and recovery slow (Fig. 3). More frequently a rhythmic component is superimposed on the tonic contraction; swimming movements appear, with excursions towards one side if the stimulus is not applied symmetrically. Here again adaptation is rapid and the swimming beats tend to become symmetrical (Fig. 4). Prolonged bilateral stimulation causes in all preparations the appearance of symmetrical swimming beats, which may become more and more persistent as the preparation recovers from the operational shock (Fig. 4).

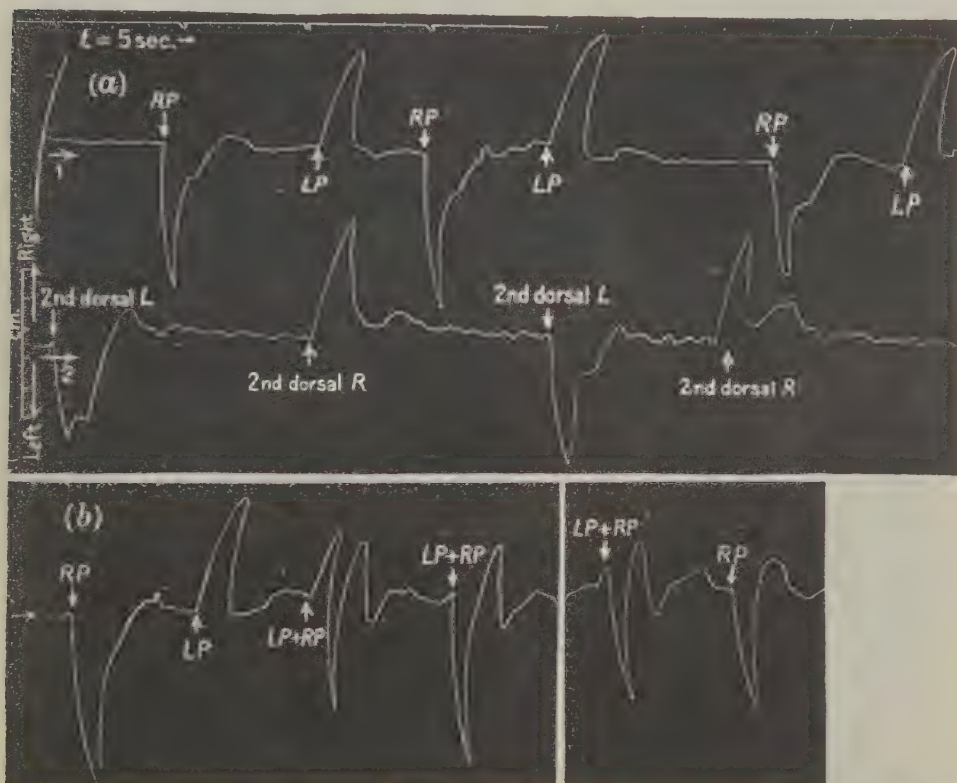


Fig. 2. (a) Response recorded from the first dorsal fin of an inactive spinal preparation of *Acanthias vulgaris* to lateral touch (1) at the level of the pectoral fins, alternately right and left; (2) at the level of the second dorsal fin, alternately right and left—note that the response is reversed. (b) The same preparation responding to successive and synchronous stimulation at the level of the right and left pectoral fin. Note the biphasic response after synchronous stimulation.

It seems obvious to associate the initiation of the swimming response with a withdrawal reflex—withdrawal from a tactile or nociceptive stimulus. The nature of the response, however, also depends on the method of applying the stimulus. Thus while one gentle stroke with a camel-hair brush causes withdrawal of the stimulated region, which may be followed by swimming (Fig. 5 B), a more persistent tickling with the brush of a localized area produces at first only slight movements, followed very suddenly by a violent 'jerk' (Fig. 5 A), which may be repeated and has then the appearance of a 'shaking reflex'. It seems that rotational movements along the long

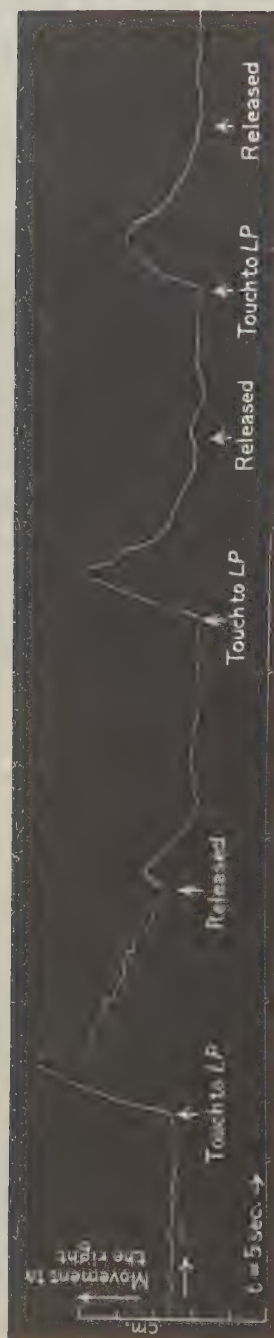


Fig. 3. Continuous touch to the left pectoral fin (*LP*) of a spinal *Acanthias vulgaris* causes a tonic reflex posture of exceptional duration. Note that adaptation to the stimulus appears rapid, and recovery slow. Recorded from the first dorsal fin.

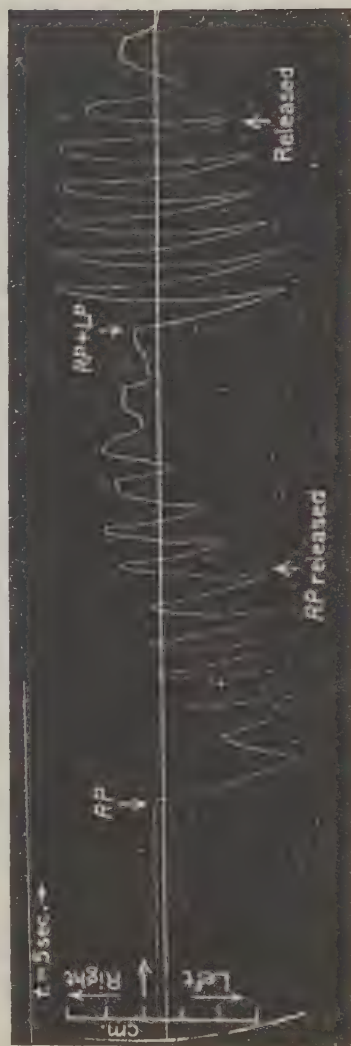


Fig. 4. Continuous touch to the right pectoral fin (*RP*) of an inactive preparation of *Acanthias vulgaris* causes asymmetrical swimming beats, which tend to become symmetrical. Continuous and simultaneous touch to the right and left pectoral fins (*RP + LP*) produces symmetrical swimming beats. Recorded from the first dorsal fin.

axis of the body are associated with it. It is conceivable that this response—which also occurs during swimming—has a functional significance in the removal of ectoparasites which are in the process of attachment.* The experiments reported below, however, refer mainly to the swimming type of response.

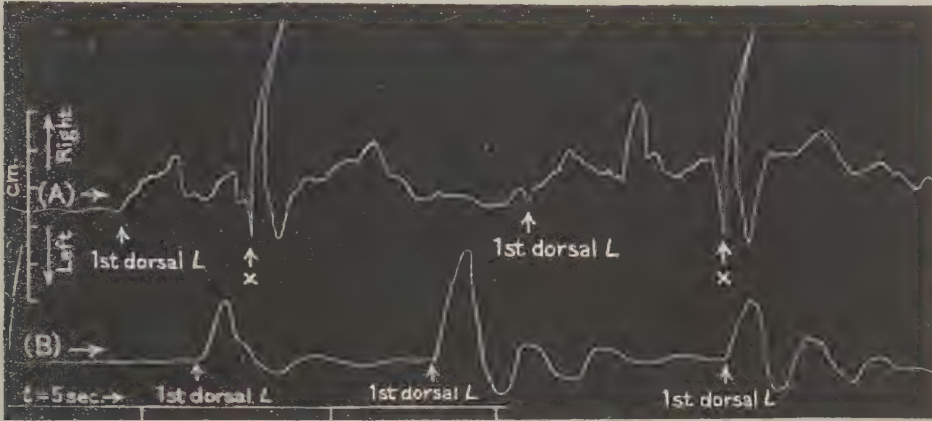


Fig. 5. Response of an inactive spinal preparation of *Acanthias vulgaris*, recorded from the first dorsal fin (A), to persistent tickling with a camel-hair brush of a localized area to the left of the first dorsal fin. Note irregular movements, and after an initial bending towards the side of stimulation (left) a violent jerk (x) away from it, rapidly followed by return. (B) One gentle stroke with a camel-hair brush at the same level produces a withdrawal of the stimulated region, followed by some beats of the swimming type.

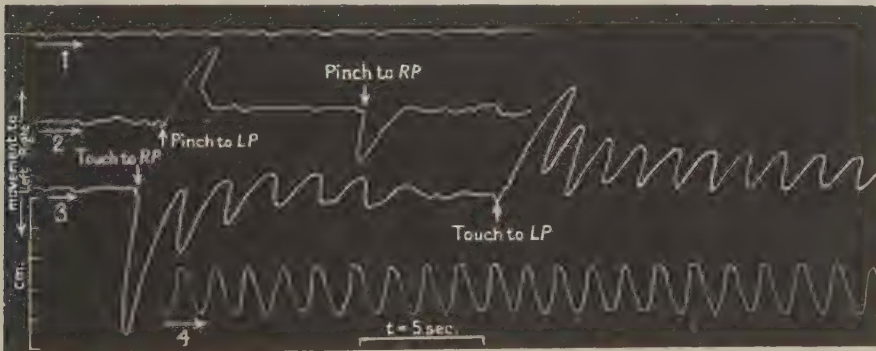


Fig. 6. Reactions of a *Scyllium canicula* on recovery from spinal transection under urethane anaesthesia. (1) Regular breathing appears; (2) single responses evoked through a pinch to the left and to the right pectoral fins; (3) rhythmic response after touch to the right and left pectoral fins; (4) the persistent swimming emerges.

Active preparations

When the spinal cord of a dogfish is transected behind the medulla, the preparation fixed by the snout and free from contact, the course of subsequent events is extremely uniform. Fig. 6 may serve as an illustration. As the animal recovers from

* *Obelia* as well as *Balanus* and some Crustacean parasites have been observed on *Acanthias*.

the anaesthetic breathing movements are the first to appear; the animal fails as yet to respond to exteroceptive stimulation. In the second stage a strong pinch to the more sensitive parts of the body elicits a single response. Somewhat later this response may be followed by a variable number of swimming beats—the number increasing as time goes on. Finally, either in response to a stimulus or without any accountable reason, the persistent swimming emerges. The time scale of events may take a few minutes or several hours, but not a single case has been observed in which the permanent rhythm failed to appear.

In an active preparation of *Acanthias* the amplitude of the beat as recorded from the first dorsal fin is about 2 cm., in *Scyllium* about 4 cm. The frequency is for *Acanthias* approximately 30–35 beats per minute, and about 40–42 for *Scyllium*; it is, however, likely to vary with external and internal conditions, e.g. temperature, age of preparation, etc.

If, on the other hand, the preparations were left in the tank after spinal transection, then their behaviour varied considerably, ranging between the type as described by ten Cate & ten Cate-Kazejewa (1933) to others which corresponded more closely to the account given by Gray & Sand (1936); in the former case they remained immobile at the bottom of the tank, and only occasionally began to swim, either 'spontaneously' or after excitation; in the latter case they exhibited an incessant swimming rhythm. The reasons for this difference are not quite clear, but attention should be drawn to Bauer's (1926) discovery of certain areas on the fish body which may have an inhibitory effect on the swimming movements when suitably stimulated. *Acanthias* tended to be less active, and normally rested motionless on the bottom of the tank, whereas most individuals of *Scyllium* displayed the swimming movements.

As there appeared to be a marked contrast between the behaviour of these dogfish and others which were suspended from the snout, it seemed reasonable to suppose that the state of inactivity was caused by the touch to the surface of the animal. When the spinal *Acanthias*, which rested at the bottom of the tank, and the inactive specimens of *Scyllium* were held by the snout, either in a vertical or horizontal position, they invariably resumed their incessant swimming. However, as soon as a glass plate was gently placed against the ventral side of the animal the swimming ceased, in some preparations almost immediately, in others after some delay (Fig. 7). However, some—notably *Scyllium*—continued to swim. The fact that this response is the result of inhibitory action, and not caused through mechanical conditions, is clearly demonstrated by the observation that when the glass plate is carefully removed, the fish tends to remain inactive. A clear example of this behaviour is recorded in Fig. 8. This fish had been observed swimming without interruption for many hours. When the glass plate was held against the ventral surface the swimming ceased, but was subsequently resumed when the plate was withdrawn after a contact of about 10 sec.; the swimming then started with some beats of small amplitude and low frequency. If, on the other hand, the glass plate was held against the body for about 20 sec. or more, and then removed, the fish remained inactive. The swimming, however, could again be released by a single,

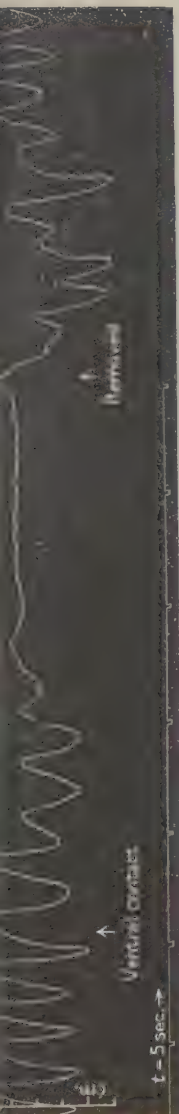


Fig. 7. Inhibition of the persistent swimming rhythm of *Scyllium canicula* by bringing a glass plate in contact with its ventral surface. The rhythm emerges again when the glass plate is removed.

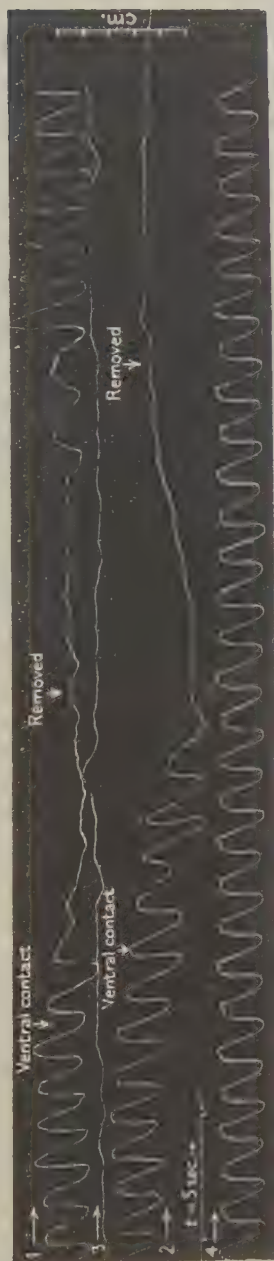


Fig. 8. A spinal preparation of *Acanthias vulgaris* shows a persistent locomotory rhythm as long as it is free from contact. (1) The rhythm can be inhibited by lifting a glass plate to the ventral side. When the glass plate is removed after about 10 sec. the rhythm starts off again. (2) When the glass plate is left in contact with the ventral surface for about 20-25 sec. or more, the fish remains inactive after removal of the plate (3). (4) A gentle touch starts the persistent rhythm again.

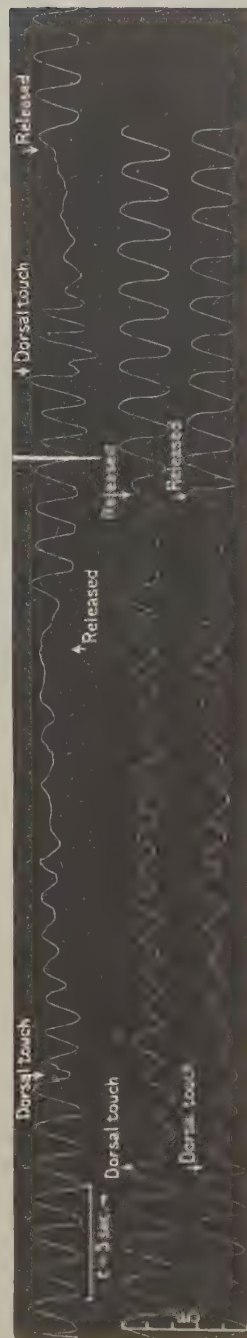


Fig. 9. Cessation of swimming or reduction of the amplitude in a spinal *Acanthias vulgaris*, caused through a gentle touch with a camel-hair brush in the exact dorsal median line between the pectoral fins.

gentle, tactile stimulus, and it persisted until a further inhibitory stimulus was applied. This experiment was repeated many times, extending the states of activity and inactivity to several hours, and only once was the previously inhibited fish found swimming after 5 hr. without the application of any intentional releasing stimulus.

This behaviour is just one instance of the many interesting analogous reactions observed by Sherrington (1904) in the spinal dog. Sherrington writes: 'The mere gentle passive arrest of the moving limb often leads to the subsidence almost immediately of the rhythmic reflex either of step or scratch, the reflex being found to be no longer in operation on release of the limb after a brief arrest.'

The observations on the dogfish clearly indicate that (i) a diffuse touch to the ventral surface can inhibit the persistent swimming, (ii) the state of inactivity may persist unless a releasing stimulus be applied, and (iii) once the releasing stimulus has been applied the state of activity is maintained. As the state of either activity or inactivity is maintained for prolonged periods under equal external conditions, and as that state is determined by the initial stimulus, it is hard to avoid the conclusion that in the case of activity the excitatory effect of the releasing stimulus sets up a sequence of re-exciting processes (such as proprioceptive reflexes or central self-exciting cycles) which are the further cause of the persistence of movement.

Gray & Sand (1936) report that some preparations cease to swim when they are turned on the back, touching the tank, and that these preparations resume swimming when returned to their normal position. No attempt has been made to repeat this experiment, but many specimens of spinal *Acanthias* have been found in the tank resting on the back without any signs of swimming movements. As has been mentioned before, localized touch to almost any part of the body accentuates the swimming. The only exception which occasionally was found to stop swimming, or more often to reduce the amplitude of the swimming beat, was a gentle touch with a camel-hair brush in the exact dorsal median line at the level of the pectoral fins (Fig. 9). This caused a marked ventral depression of the body in the stimulated region, and a lifting of the pectoral fins. The response is tonic in itself, and owing to the rigidity which it produces in the body is likely to reduce the amplitude of the swimming. According to Bauer's description inhibition can be obtained regularly through gentle, blunt touch to the anal fin (not present in *Acanthias*), and a ventral zone slightly anterior to the tail fin, occasionally also by touching the back.

I have not been able to confirm other types of inhibitory action as described by previous authors. Neither *Scyllium* nor *Acanthias* ceased to swim after either touching, pinching or pressing in a variety of ways either of the dorsal fins (cf. le Mare, 1936). The response was invariably accompanied by acceleration and augmentation of the rhythm (Fig. 10).

Apart from the superficial cutaneous inhibitory effect, cessation of the rhythm has also been demonstrated to occur after application of strong pressure to the body. On this point there is general agreement, and little new can be added. However, I would hesitate to group these two phenomena of arrest closely together. Cessation of swimming on application of deep pressure is preceded by a rhythm of

wider amplitude but slower frequency as compared with the normal swimming rhythm; this reaction often lasts several minutes. The power of the beats is considerable; cessation, when it occurs, has the appearance of fatigue. The general impression conveyed by this response is that it is the composite picture of a number of events, caused by simultaneous but differential contractions of the myotomes at the same level; one might assume reinforcement to take place in response to isometric conditions. It is noteworthy that preparations inhibited through ventral touch, when subjected at the same time to strong pressure, nevertheless show the same succession of reactions as preparations freely suspended in water (Fig. 11). On release accelerated and augmented movements emerge, followed by a period of

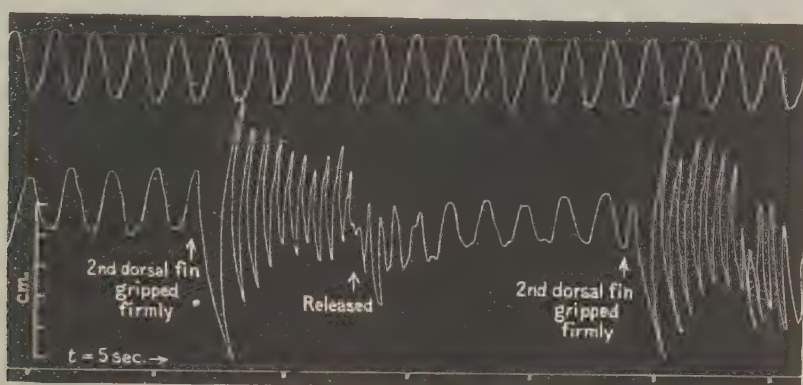


Fig. 10. Upper tracing: normal swimming rhythm of a spinal *Acanthias vulgaris*. Lower tracing: augmentation and acceleration after gripping the second dorsal fin.

swimming beats, despite the continuous ventral contact. If simultaneously with the application of strong pressure to the body a further nociceptive stimulus be applied, e.g. a clip attached to the tail, the frequency of the original response is increased; it is, however, not as high, as it is after the attachment of the clip to an otherwise undisturbed dogfish. The frequency of the two responses seems to integrate arithmetically—as if the effects were added and divided by two. Similar reactions have been recorded in the eel by von Holst (1935 a).

The question seems justified whether the rhythmic component of the response which appears on application of strong pressure to the body may be caused by a nociceptive stimulus, acting simultaneously with another stimulus which has the tendency to arrest or retard the movement. On the basis of two different sensory mechanisms underlying this response, it may be intelligible that after fatigue of one of them the response emerges in a different form. Thus if after repeated application of a strong clamp the nociceptive elements drop out, only arrest will take place due to the pressure. This type of reaction has been recorded by Gray & Sand (1936). The nature of the rhythm as it ensues in a fresh preparation after the release of the pressure (Fig. 11) is suggestive of a participation of a nociceptive stimulus, while the retarding effect may involve deep pressure receptors, or proprioceptors responding

to isometric conditions. A possibly related response has been recorded from *Scyllium* to the denervated tail of which a string was attached. A gradual increase of longitudinal tension applied by the string produced a gradual slowing down of the rhythm (Fig. 12), and an increase in the amplitude and force, until all movement was arrested. The most likely suggestion is that in this case it is the more isometric contraction which causes the alteration in the rhythm. This is surprising in view of the fact that von Holst (1935*b*) has demonstrated that there is no evidence to show that isometric conditions as such alter the normal swimming rhythm; von Holst produced mechanical rigidity over a considerable portion of the vertebral column of an eel, without markedly affecting either the swimming movements or the co-ordination between the anterior and the posterior end.

Von Holst's statements about the accelerated rhythm following a nociceptive stimulus do not seem altogether satisfactory. While in one experiment (1934) he suggests that it is a special nociceptive reflex bearing no relation to swimming, in another experiment (1935*b*) he releases the swimming rhythm through a strong pinch to the pectoral fins in an otherwise de-afferentated tench. Although in the dogfish, after the application of a strong stimulus, the change from regular swimming to an accelerated rhythm may be very sudden, the response merges without a perceptible break back into the normal swimming rhythm (Fig. 13); this may be taken as an indication that the same nervous elements form an integral part of the mechanism in both cases.

Von Holst also claims that the rhythmic-automatic neurones are quite distinct from the motor-neurones, and that the latter are excitable through reflex stimulation, without the participation of the former. It might therefore be expected that if a reflex be released in an actively swimming dogfish the result may be one of strict superposition of an independent automatic rhythm to which an equally independent reflex response is added. The great regularity of the swimming movements in the spinal dogfish makes this preparation particularly suitable for a study of the effects of transitory stimuli on the subsequent performance. Through an appropriate slight touch any single beat can be augmented, accelerated, suppressed or reversed at any phase of the movement (Fig. 14). When the rhythm emerges again with the next regular beat—it can be of the same or nearly the same amplitude and frequency as prior to the stimulation—but in nearly every case which has been recorded it is out of phase with the rhythm as recorded before the stimulation was applied. The re-setting of the rhythm after a very short and feeble stimulation shows how susceptible the rhythmic elements are to outside influence. At the same time there appears a definite break in the response whenever the rhythm emerges again after reflex modification, which may point to a certain degree of independence.

As has been shown above, the application of a localized stimulus may cause anything from a purely local response to a rapid spreading of a reflex posture over the body. If a stimulus be applied to an actively swimming dogfish, exhibiting a dynamic reflex posture, it will depend on the site of stimulation and the phase of the movement, whether the dynamic and the induced postures will be competitive, synergic, or to some extent out of phase. The nature of the response will also depend



Fig. 11. Spinal preparation of *Acanthias vulgaris*, the swimming movements of which are inhibited through ventral touch, responding to temporary application of very strong pressure to the body in the region of the pectoral fins.

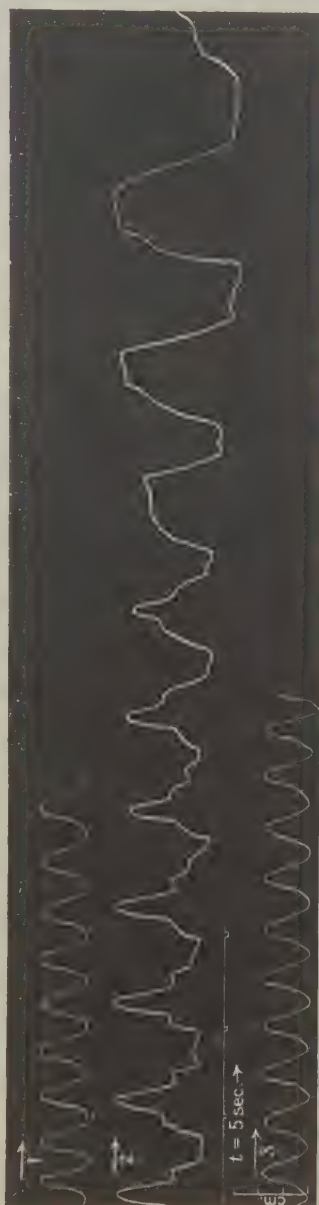


Fig. 12. Alteration of the swimming rhythm in response to gradually increasing pull applied to the denervated tail of a spinal *Scyllium canicula*. Eventually the rhythm stopped. The tracings above and below show the normal swimming rhythm as recorded before and after the application of the pull.

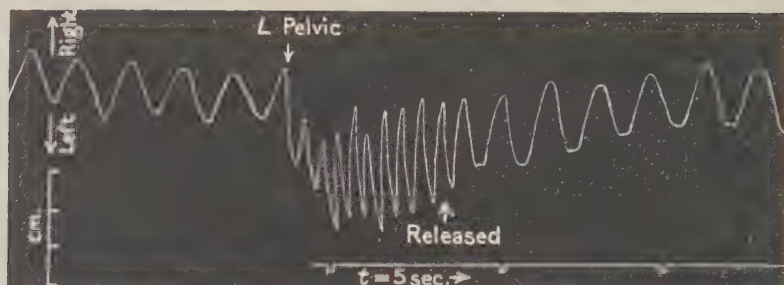


Fig. 13. Response of a spinal *Acanthias vulgaris* to a pinch applied to the left pelvic fin. The accelerated and augmented rhythm merges back into the normal frequency and amplitude of swimming without any noticeable break.

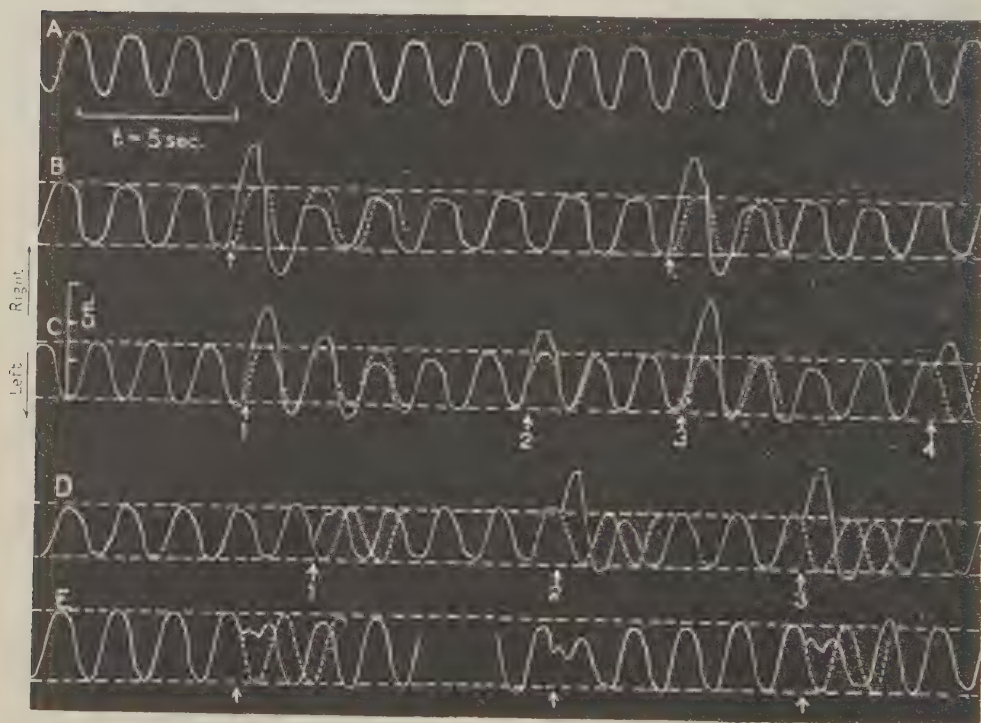


Fig. 14. Transitory reflex stimulation (a gentle touch near the left pectoral fin) causes a resetting of the phases of the swimming rhythm in a spinal *Acanthias vulgaris*. The tracings show that the effect of a brief stimulus depends on the momentary phase of movement: (A) normal, undisturbed swimming rhythm; (B) augmentation, acceleration and rebound of a single beat; (C) augmentation with little or no acceleration; in this instance the swimming rhythm continues more or less at the original frequency (1, 2, 3) because the stimulus was adjusted so as to extend over both phases (right and left) of the swimming stroke; when the stimulus was applied somewhat later, and coincided with the beginning of the swimming beat to the left (4), the rhythm is at once thrown out of phase; (D) (1) reversal without augmentation; (2) and (3) reversal with augmentation; (E) temporary arrest.

on the strength and duration of the stimulus. Thus if the induced posture is in competition with a given phase of the movement the result can be (a) a retarding effect, (b) temporary arrest (Fig. 14E), (c) reversal (Fig. 14D). If the two phases are synergic an early application causes augmentation and acceleration, often associated with rebound (Fig. 14B); if, on the other hand, the stimulus is extended until the phase of movement reaches the turning point, augmentation may occur without acceleration and without rebound, and provided the stimulus extends equally in duration and strength over two phases of a swimming stroke, the frequency of the rhythm may remain unaltered (Fig. 14C). The significance of these phenomena will be referred to later. A feeble, localized stimulus does not necessarily impress a posture over the entire length of the body. If it is applied to an actively swimming dogfish, only the posture nearest to the stimulus will be modified for a short period. After that period, when the effect of the stimulus has faded out, the two parts of the body, those affected by the stimulus and the unaffected ones, reintegrate to form a new swimming wave. The break in the tracing appears to indicate that this process is rather sudden, probably because the effect of a feeble stimulus wears off rapidly (see Fig. 1).

Fin reflexes

It appears that the fin reflexes in the dogfish have not, hitherto, been subjected to anything but very casual examination. Apart from observations on the clasper reflex, it is stated that the pectoral fins act as inclined planes (Bethe, 1899; le Mare, 1936), that the dorsal fins are bent away from any stimulus applied near the base (le Mare, 1936; ten Cate, 1934). However, the responses of the fins are not quite as monotonous as one might gather from these descriptions, certainly not in *Acanthias*, and probably not in *Scyllium*. There are indications of not very well developed, but nevertheless distinct, biphasic or rhythmic responses to a single exteroceptive stimulus.

(1) *Dorsal fins*. The responses of the two dorsal fins in *Acanthias* are essentially similar, and have been recorded by attaching a recording lever to the posterior margin of the fin. The nature of the response is determined by the site of stimulation; the receptive fields extend over a large part of the body, and partly overlap. If the stimulus is feeble the response is restricted to one or both dorsal fins; if the strength is increased, movements of the trunk may be associated with it. Stimulation along the base of either dorsal fin causes two distinct types of reaction, depending on the level of application. Anteriorly to the fin a slight touch with a camel-hair brush or straw causes a bending of the fin away from the side of stimulation; this response may be sustained. Posteriorly it causes a very rapid flick towards the side of stimulation, after which the fin returns to its initial position (Fig. 15). If the latter stimulus is more sustained, the response may be either repeated or reversed, and followed by a beat of the body musculature. The response of the fin itself may, however, be more sustained, and in such cases a quivering motion can be noticed on the posterior margin of the fin (Fig. 15B). This quick response is always more sustained when the fin engages the straw or brush which causes the stimulus.

It seems reasonable to suppose that this is due to reinforcement produced by more isometric conditions, analogous with similar reactions in the tetrapod limb. The quivering of the fin margin can also be observed when the stimulus be applied anteriorly, causing a bending to the contralateral side.

It has been suggested that the movements of the fins during active locomotion may be governed by the proprioceptors of the trunk. An alternative theory suggests that 'their movement may be governed by a similar or the same internal automatic rhythm which regulates the swimming rhythm of the trunk' (le Mare, 1936). In

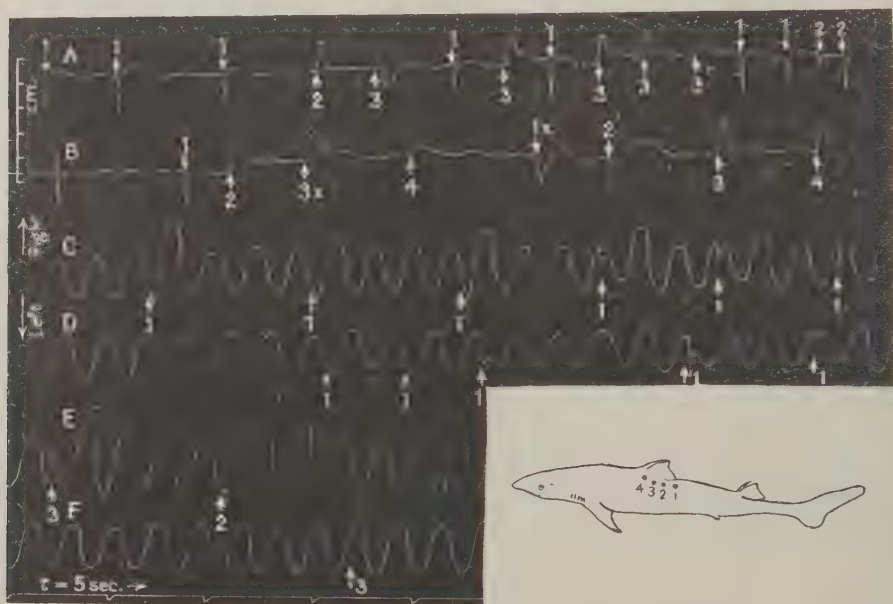


Fig. 15. Dorsal fin reflexes in a spinal *Acanthias*, recorded from the posterior border of the fin. The numbers in the tracing correspond to the site of stimulation along the base of the dorsal fin as indicated in the outline figure. Stimulation, a gentle touch, was applied to the left of the fin. Note that stimulation at 1 causes a quick beat towards the side of stimulation. Stimulation at 3 and 4 invariably produces a more prolonged beat to the contralateral side. When stimulation was applied at 2 the response was either identical with one of the two previous reactions, or represented a combination of the two. A and B show the reactions as recorded from an inactive preparation; C-F the same reactions recorded at various phases of the swimming beat from actively swimming preparations. The quivering motion of the posterior border of the fin is recorded in the more sustained reactions marked (x).

either case the influence of the proprioceptors, or of the supposed internal rhythm can be certainly overruled by local reflexes, because the reflexes described here can be evoked in any phase of the swimming movements, and then appear superimposed on the swimming rhythm (Fig. 15 C-F).

It does not appear difficult to assess the probable biological significance of these two reflexes. If a light object is placed posteriorly within the action radius of a dorsal fin, it is removed by a quick beat. The receptive field of this reflex, however, extends considerably beyond the action radius.

If, on the other hand, an object touches the back of an actively swimming dogfish anteriorly, and towards one side of the dorsal fin, it is likely to be swept backwards and engage the fin; consequently the fin is bent to the contralateral side.

(2) *Pectoral fins.* The range of movement of the pectoral fins in the dogfish is undoubtedly limited; the fins can be elevated and depressed, abducted and adducted, and to a small extent they are capable of rotation. Touch near the base of the anterior border of a pectoral fin causes elevation and adduction (retraction) of the anterior margin and depression of the posterior lobe (rotatory movement). In fresh preparations this response may be repeated up to five times. From a receptive field extending from the posterior border of the pectoral fin to the level just beyond the first dorsal fin, an elevation of the posterior lobe can be produced. The responses of the two pectoral fins can be identical or opposed according to the site of stimulation. Thus both pectoral fins are elevated posteriorly when the back of the animal is touched; they are both depressed in response to ventral touch. This response also occurs when one of the fins and the adjoining segments are de-afferentated. If the ventral stimulus is moved towards the posterior border of one of the fins, depression changes to ipsilateral elevation, while the contralateral fin is still being depressed. All these responses can probably be interpreted as leading to an avoiding reaction through changing the course of swimming of the animal. On the other hand, if in *Scyllium* a finger is placed near the posterior angle of insertion between the body and the fin, the fin is first elevated and then adducted, the placoid scales scraping noticeably against the finger; this response may be repeated several times. It seems legitimate to suppose that this reaction is a primitive precursor of the scratch or cleaning reflex.

DISCUSSION

The numerous recent endeavours which try to explain swimming movements of fish, and locomotory movements in general, on the basis of an essentially central mechanism, have led to a complicated interpretation, which does not always appear plausible. It is difficult to visualize the reasons why the medulla, the rhythmic activities of which in the isolated state have been related to the swimming rhythm, should exert a *steady and continuous* effect on other elements in the spinal cord which are termed the 'automatic-rhythmic cells', and which in turn are said to affect rhythmically the 'motor-cells' (von Holst, 1934-9). No conclusive evidence appears to have been produced to show the existence of an independent automatic-rhythmic process on to which reflex responses may be superimposed through direct excitation of the motor-cells. As long as the animal is at rest neither the strength of any locomotory reflex nor the reflex time have been demonstrated to alter rhythmically in such a way that it might appear reasonable to ascribe such changes to a concealed, continuous, inherent rhythm in the central nervous system playing a 'predetermined score' (Weiss, 1941).

It is difficult not to ascribe to reflexes a very important role in swimming, although there is overwhelming evidence to show that the undulatory posture evoked through stimulation does not spread over the body of a fish as a reflex chain

from segment to segment. The formation of the undulatory posture with primary and secondary regions of contraction must be considered essentially as *one* reflex; it is determined by the stimulated receptive field, and the central and peripheral pathways. In this process the spinal cord acts as an entity.

All this, however, does not exclude the possibility that the normal passage of the undulatory posture (swimming) is brought about by a temporal chain of processes, which also involves proprioceptive excitation, and may therefore be considered as the integration of two distinct types of reflex. Little is known of the exact mode of interaction, but the work of Fessard & Sand (1937) indicates the probable occurrence of proprioceptive reflexes during active locomotion in fish. Once the undulatory posture has been established it is, therefore, most likely that the pattern of the spatial arrangement of these impulses corresponds in some way to the pattern of the existing primary and secondary contractions which form the undulatory posture.

SUMMARY

1. Body and fin reflexes in the spinal dogfish, *Scyllium canicula* and *Acanthias vulgaris*, are described.
2. A reflex posture can be induced in inactive spinal preparations through localized exteroceptive stimuli. The location of the primary and secondary contraction areas is determined by the site of stimulation.
3. Spinal preparations of *Scyllium canicula* and *Acanthias vulgaris* display a persistent locomotory rhythm as long as they are free from contact.
4. Diffuse touch to the ventral surface of a spinal preparation has an inhibitory effect on the swimming movements. Some dogfish remain immobile after the ventral contact has been discontinued, but resume their persistent swimming after application of a gentle exteroceptive stimulus of short duration.
5. Through feeble transitory stimuli any individual swimming stroke can be retarded, temporarily arrested, reversed, accelerated and augmented. The reaction depends on the site of the stimulation and on the momentary phase of the swimming movement at which it is applied.
6. The rhythm emerging after the application of a transitory stimulus is, as a rule, out of phase with the rhythm as recorded prior to the application of the stimulus. Therefore the response cannot be interpreted as resulting from a superposition of an independent automatic rhythm integrating with a reflex, but must be considered as an interaction of two equal and mutually dependent processes.

I wish to express my thanks to Prof. J. Gray, F.R.S., for the interest he has taken throughout the course of this work. The experiments were performed while holding a Cambridge University Table at the Laboratory of the Marine Biological Association in Plymouth, and the Marine Station, Millport, of the Scottish Marine Biological Association. I am indebted to the Directors and their staffs for hospitality and for considerable assistance.

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THE NEUROLOGICAL BASIS OF THE LOCOMOTORY RHYTHM IN THE SPINAL DOGFISH (*SCYLLIUM CANICULA*, *ACANTHIAS VULGARIS*)

II. THE EFFECT OF DE-AFFERENTATION

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(With Thirteen Text-figures)

INTRODUCTION

A critical examination of the various experiments in support of the theory of a central spontaneous and automatic drive behind rhythmic locomotory movements shows that, although these experiments may be considered as suggestive, they are by no means conclusive. (i) So far as is known no direct connexion has been demonstrated between the slow changes of electrical potential in the central nervous system—alleged to represent the central drive—and the impulses observed in motor nerves. (ii) It is often quoted that in all animals so far examined (with the sole exception of some mammals), extensive and even complete de-afferentation does not alter the basic patterns of co-ordination. But it is still a matter of dispute whether or not afferent inflow, however limited, constitutes an essential part of the mechanism which maintains locomotory rhythms—either as a pacemaker or by keeping the central excitatory state at an appropriate level.

It is well to remember that complete de-afferentation of the body can in most cases produce no conclusive evidence, because as soon as the afferent excitation from the cranial region is cut off by a post-medullary transection of the spinal cord, the animal, even if not de-afferentated, will no longer display a locomotory rhythm with any regularity; the medulla, on the other hand, is an important sensory centre. As mentioned previously, the exception to this rule is supplied by the dogfish, which, after the spinal cord has been severed behind the medulla, shows for long periods a persistent locomotory rhythm.

The experiments described in the preceding paper (Lissmann, 1946) demonstrate the profound, though apparently mostly temporary effect, which reflex stimulation may have on the swimming rhythm of the dogfish. However, the observation of persistent inactivity after withdrawal of an inhibitory stimulus, and persistent activity after application of a single releasing stimulus, suggests that the maintenance of the normal swimming rhythm may be dependent on re-excitation, the most obvious source of which may be suspected in the peripheral proprioceptors. To test this possibility a series of de-afferentation experiments was carried out.

So far as is known no complete de-afferentation of the somatic musculature has been attempted in fish, although von Holst (1935) has shown that after severance of

all except the anterior dorsal roots the locomotory rhythm can be elicited in a tench by a pinch to the pectoral fins. This author, on the other hand, has also demonstrated the profound influence of one locomotory rhythm upon another, and found that the pectoral fin rhythm has often a dominant position. Gray & Sand (1936) cut all the dorsal roots in a dogfish over a length of 5 in. in the region of the pectoral fins. This animal remained at rest at the bottom of the tank unless stimulated; the state of relative inactivity was attributed to the operation and to the exposure of the spinal cord.

METHOD

The operation of partial or complete de-afferentation in the dogfish was performed as follows. The animals, anaesthetized in 1 or 2% ethyl urethane, were fastened to an operating board, and a current of oxygenated sea water passed through the mouth. The vertebral column was then exposed through a longitudinal median incision along the dorsal septum, and the wound kept open by hooked pins attached to threads which exerted a slight lateral pull. After this the cartilaginous roof of the neural arches was removed in one piece by two lateral cuts with fine spring scissors. To obtain a clearer view, and to prevent premature formation of blood clots, the nerve cord was constantly subjected to a fine jet of elasmobranch Ringer. Transection of some or all dorsal roots (numbering in both species approximately sixty-five pairs down to the base of the tail) can be executed without much difficulty. It has been found helpful, however, to insert into the muscles at the level of each transection a fine insect needle; from the equal spacing of these needles it can easily be detected whether a pair of roots has been overlooked. The operation lasted several hours when all roots were severed, and, from time to time, a current of urethane had to be passed through the mouth of the animal. In the tail region, where transection of the dorsal roots is difficult on account of their small size, the spinal cord was transected either before or after the main operation, usually at the level of the ventral lobe of the tail fin, i.e. about eight pairs of roots behind the posterior border of the second dorsal fin. A similar transection was performed in the post-medullary region. The wound was then closely stitched up, sometimes enclosing between the stitches strands of cotton-wool soaked in vaseline. After this operation the animals were kept alive and under observation for several days. The possibility of releasing locomotory rhythms before and after de-afferentation through electrical stimulation was explored with the aid of an induction coil. The spinal cord was either lifted on to two steel electrodes, or the electrodes were placed laterally near the cord. Single shocks could be applied by operating a tapping key; an interrupter was used for higher frequency stimulation.

EXPERIMENTS

(1) *The exposure of the spinal cord* in its entire length did not abolish the persistent rhythm either in *Scyllium* (four specimens) or *Acanthias* (two specimens) (Figs. 4a, 5c, 12a). In fact, animals which were rather sluggish after spinal transection showed at times greater activity after the cord had been exposed.

(2) *Partial de-afferentation*. Bilateral de-afferentation from the level of the spinal transection to the base of the first dorsal fin, involving the severance of about thirty-five pairs of dorsal roots, or de-afferentation of the posterior region, from the first dorsal fin to the base of the tail, was executed on a number of animals of both species. On recovery from the operation all animals displayed the characteristic rhythm. The contraction of the desensitized musculature was quite obvious and could be ascertained by holding the de-afferentated region between the fingers. These preparations responded like normal fish to reflex stimulation when this was applied to the sensitive part of the body. Similar partial de-afferentation has been carried out on several specimens of *Scyllium*, in which the spinal cord had not been transected. Apart from the fact that these animals showed the intermittent type of swimming, characteristic of normal dogfish, the reactions were identical with those of the spinal preparations.

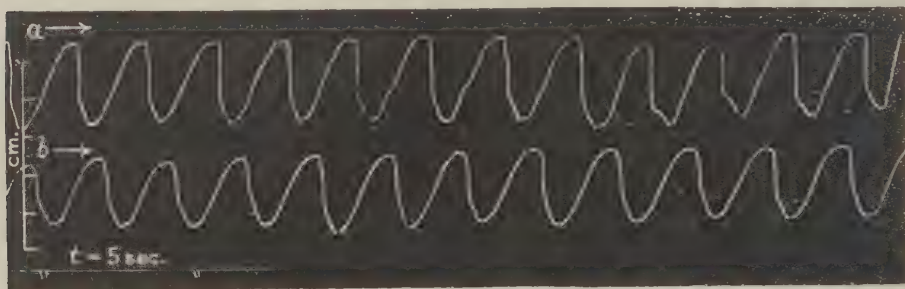


Fig. 1. (a) The swimming rhythm of a spinal *Acanthias vulgaris*. (b) The swimming rhythm of the same preparation after complete unilateral de-afferentation (on left).

In one *Acanthias* all dorsal roots were transected on the left side. The persistent rhythm emerged 1 hr. after the operation; it was found to be symmetrical, and in amplitude and frequency practically indistinguishable from the rhythm as recorded prior to the operation (Fig. 1). The sensitivity extended to the exact ventral median line along the whole length of the body.

(3) *Extensive de-afferentation*. Some of the partly de-afferentated preparations described above were subjected to a second operation, and most or all the remaining dorsal roots were cut. In the preliminary stages of this investigation an attempt was

(Legends for Figs. 2, 3 and 4)

Fig. 2. *Scyllium canicula*. (a) The persistent swimming rhythm after spinal transection. (b) The same preparation, de-afferentated except for the tail and four pairs of dorsal roots in the region of the first dorsal fin, responding to a pinch applied to the dorsal fin by a series of swimming strokes, which also involve the desensitized regions of the body; the swimming does not persist. (c) Following repeated nociceptive stimulation to the tail and the first dorsal fin, a slow rhythm occasionally emerges for short periods.

Fig. 3. A spinal *Scyllium canicula*, completely de-afferentated except for one pair of dorsal roots in the region of the second dorsal fin and the tail, responding to a continuous series of pinches applied to the tail by a slow rhythm which does not persist.

Fig. 4. (a) The persistent swimming rhythm of a spinal *Scyllium canicula*, recorded immediately after exposure of the spinal cord in its entire length. (b) After complete de-afferentation, except for the tail, a clip or a pinch with forceps produces a static reflex posture, but no rhythmic response.

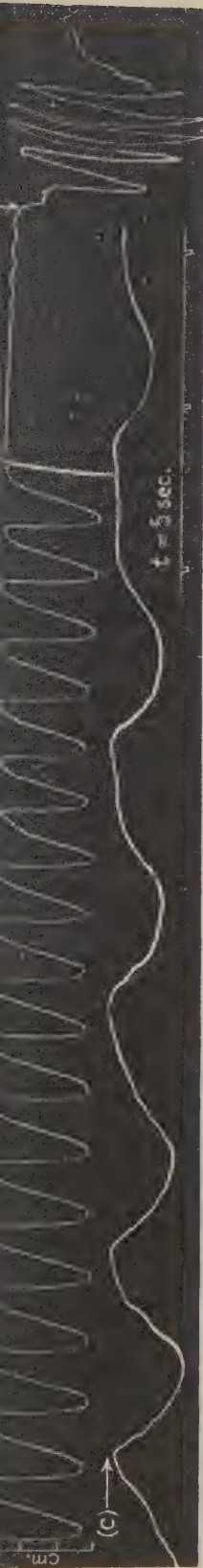


Fig. 2.



Fig. 3.



Fig. 4.

made to de-afferentate completely two specimens of *Scyllium*, the spinal cord of which had previously been exposed. The attempt, however, was not successful on account of the blood clot. Some roots could not be traced, and after the operation both animals showed small patches of sensitivity and a feeble rhythm.

In one *Scyllium* all dorsal roots, except four pairs in the region of the first dorsal fin and those in the tail, were transected. On recovery the animal showed no rhythm, but a strong pinch to the first dorsal fin invariably produced up to 10 beats of an amplitude and frequency comparable to the response evoked by a nociceptive stimulus applied to a spinal fish (Fig. 2*b*). This rhythm usually did not persist, but on one or two occasions, after periods of violent excitation, both from the tail and the first dorsal fin, a very slow rhythm emerged for a short period (Fig. 2*c*).*

In one *Scyllium* all roots except those in the tail and one pair in the region of the second dorsal fin were cut; this abolished the persistent swimming rhythm. A pinch applied to the tail or to the second dorsal fin produced a reflex posture for a short time, but no rhythmic response. However, a succession of very strong stimuli, applied with toothed forceps to the tail, produced a slow rhythm of wide amplitude (Fig. 3), comparable in frequency perhaps to the response evoked by strong pressure to the body of a spinal fish. The reflex posture appeared to jerk backwards over the body, with each successive pinch.

Dogfish of either species, completely de-afferentated except for the tail, never showed the slightest spontaneous movement, and they never responded to tactile or nociceptive stimulation by anything but a single response, which usually threw the body into an S-shape (Fig. 4). When, instead of pinching the tail, a sharp clip was applied, the reflex posture was held somewhat longer. No rhythmic response was ever observed, either spontaneously or as a result of exteroceptive stimulation. In one instance a *Scyllium* which had not been made spinal was completely de-afferentated except for the tail. This animal did not swim, neither spontaneously, nor after stimulation.

(4) *Complete de-afferentation*. Some of the fish were de-afferentated completely in several stages, others in one single operation. None of them ever showed the slightest spontaneous movement. An additional cut through the spinal cord either anteriorly or posteriorly made the preparation twitch, but never released a response of a rhythmic nature. The muscles of these fish were normally soft and did not resist passive bending of the body. However, after some days a strong tonic contraction may develop in the somatic musculature. The body becomes extremely rigid and slightly bent. The rigidity persists when the animal dies. Similar phenomena have been described in other animals (Weiss, 1941).

The conclusions to be drawn from these experiments are:

- (i) Complete de-afferentation of the body of a spinal dogfish abolishes the persistent locomotory rhythm characteristic of unoperated spinal animals.
- (ii) If a de-afferentated region of the body is connected through the spinal cord with an intact region, both display a uniform rhythmic activity. Unilateral de-

* These results are in good agreement with the observations reported by ten Cate (1939) whose paper was available only after the completion of this manuscript.

afferentation does not alter the symmetry, frequency or amplitude of the beat to any noticeable extent.

(iii) After extensive de-afferentation the persistent rhythm disappears, but can be temporarily elicited through reflex stimulation.

(iv) Sensory impulses from the caudal (and caudal + cranial(?)) region alone are not sufficient to evoke or maintain the rhythm.

(v) A localized sensory stimulus in an otherwise de-afferentated preparation produces a static reflex figure.

(vi) The experiments suggest that the maintenance of the swimming rhythm is dependent on re-excitation, and that the periphery plays an essential role in the process of re-excitation as well as in the process of release.

(vii) The shock of the operation is not likely to account for these manifestations, as the rhythm emerges clearly when the spinal cord and the dorsal roots are exposed, but the latter not, or only partly, severed.

ELECTRICAL STIMULATION OF THE SPINAL CORD

A preliminary study has been made of the reactions which can be elicited in the dogfish in response to electrical stimulation applied to the cord. In view of the great range of possibilities of variation in the application of such stimuli, it is realized that no far-reaching conclusions should be drawn from the limited number of experiments reported here. Nevertheless, electrical stimulation applied directly to the cord has elicited some definite reproducible responses, which may be found to correspond to responses evoked by exteroceptive stimulation.

After some cursory examinations it was found easier to obtain a regular and rhythmic response, or to modify an existing rhythmic activity, when the electrodes were applied to the posterior rather than the anterior spinal cord. To keep the electrodes steady the preparations were fixed by a denervated region between the tail and the second dorsal fin; a thread was attached to the snout exerting a slight pull, thereby returning the preparation to its original position after a response. The recording lever was connected, as before, to the anterior base of the first dorsal fin.

Experiments

(1) In a spinal *Scyllium* the cord was exposed in its entire length, and, while the animal was recovering from the anaesthetic, the two electrodes were inserted laterally to the spinal cord at a level just posterior to the second dorsal fin. At a stage before any reflex response could be elicited a short burst of electrical shocks from an induction coil lasting about 0.5 sec. produced a rhythmic response of three beats, of large amplitude and low frequency, both amplitude and frequency decreasing towards the end of the response (Fig. 5). As recovery proceeded the number of beats after similar stimulation increased; decrease of amplitude and frequency was less rapid. Somewhat later the response extended over 2 min., until at last this stimulus evoked the persistent swimming movements. From then onwards a short burst of electrical stimulation increased temporarily the amplitude and frequency of swimming, which only gradually returned to normal swimming beats.

(2) Continuous electrical stimulation from an induction coil applied to the posterior spinal cord of an inactive spinal *Acanthias* elicited two distinct types of rhythmic response. (a) A weak stimulation usually caused an asymmetrical tonic contraction, on to which were superimposed very rapid beats of small amplitude, which had some resemblance to a swimming rhythm. The swimming ceased as soon as the stimulation was discontinued; there was a rebound of a tonic nature (Fig. 6). (b) When the strength of the stimulus was increased, a rhythmic response of wide

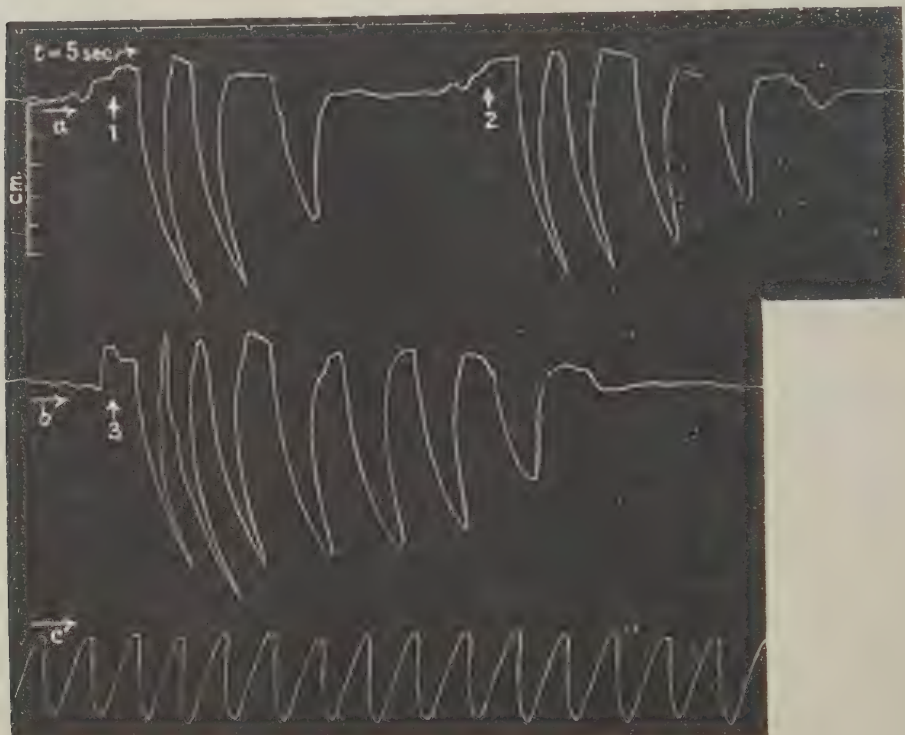


Fig. 5. Response of a spinal *Scyllium canicula*, recovering from the anaesthetic, to short bursts (0.5 sec.) of electrical shocks from an induction coil applied to the posterior spinal cord. Note that the rhythmic response continues for a considerable period after the cessation of the stimulus, the periods extending as recovery proceeds. Ultimately the swimming rhythm emerges and persists. The spinal cord of the preparation was exposed in its entire length.

amplitude and slow frequency appeared. As soon as stimulation was interrupted, the rhythm ceased, or else the small waves described under (a) appeared for a short while (Fig. 7). The two types of rhythm described above appear to be two distinct phenomena; they do not gradually change from one to the other by an increase of amplitude and reduction in frequency with a gradually increasing strength of the stimulation. At some intermediate stage they both appear and present a picture of superposition (Fig. 8). It will also be noted that with continued stimulation the frequency of the larger rhythm decreases and the superimposed smaller rhythm becomes more prominent. The frequency of the smaller of these rhythms does not

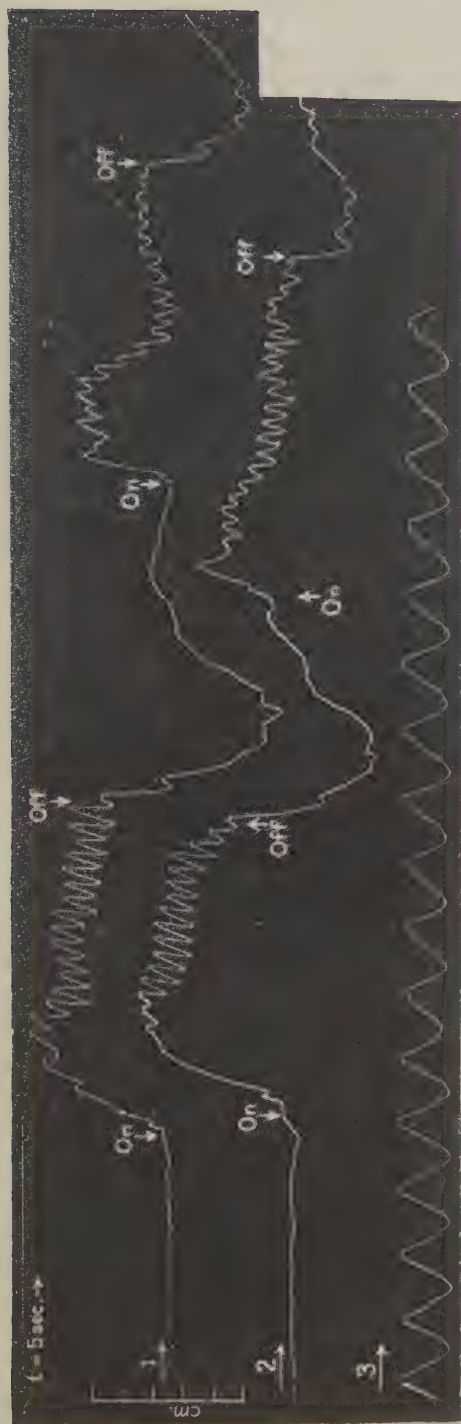


Fig. 6. Response of a spinal *Acanthias vulgaris* (swimming movements inhibited through ventral touch) to continued, feeble electrical stimulation applied to the posterior spinal cord. Note the tonic contraction, and the superimposed fast rhythm of small amplitude. Below: normal swimming rhythm of the same preparation after cessation of electrical stimulation and removal of the inhibitory stimulus.



Fig. 7. The same preparation of *Acanthias* as shown in Fig. 6, responding to electrical stimulation of increased strength and reduced frequency (5 shocks per second), with a rhythm of wide amplitude and low frequency.



Fig. 8. Response of an inactive spinal *Acanthias vulgaris* to electrical stimulation (induction coil) of intermediate strength applied to the posterior spinal cord. Note the superposition of two rhythmical reactions.



Fig. 9. Response of an actively swimming spinal preparation of *Acanthias vulgaris* to continued electrical stimulation applied to the posterior end of the spinal cord. Below: feeble stimuli quicken the rhythm and may temporarily reduce the amplitude. Above: stronger stimulation produces a secondary rhythm of wider amplitude.

appear to have any obvious numerical relationship with the frequency of stimulation; both rhythms have been obtained, once using the make and break mechanism (interrupter), the other time by operating a tapping key at a frequency of about 5 per sec.

(3) The responses of an actively swimming spinal *Acanthias* to continued electrical stimulation are essentially identical with the two responses of the inactive preparation (Fig. 9). The fish returns to its normal swimming rhythm almost immediately after the feeble stimulation has been discontinued. With increasing strength the secondary rhythm of wider amplitude makes its appearance. If the strength of the stimulus be still further increased beyond a certain limit, the animal curls round, bringing the head to the vicinity of the tail, and holding this posture in a tonic contraction as long as the stimulus is effective.

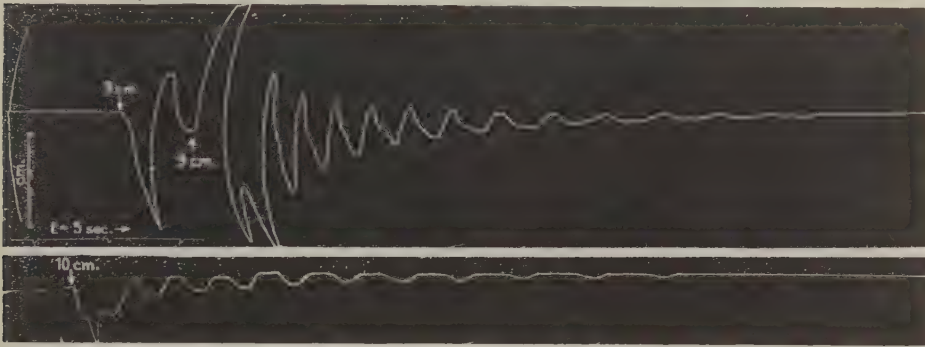


Fig. 10. A rhythmic response following a short electrical stimulation (lasting about 0.5 sec.) applied to the posterior spinal cord of a spinal *Scyllium canicula*, completely de-afferented except for the tail and one pair of dorsal roots in the region of the second dorsal fin. Note the gradual fading out of the reaction, associated with reduction both in amplitude and frequency. The relative strength of stimulation is indicated by the coil distance.

(4) When electrical stimulation was applied to the spinal cord of extensively de-afferented dogfish, it was found much easier to obtain a rhythmic response than it was in the same preparation through exteroceptive stimuli. In two cases the response persisted for a short time after the electrical stimulation had been discontinued; in both these cases, apart from the tail, either one or a few pairs of dorsal roots had been left intact in the region of the first and second dorsal fin respectively (Fig. 10). When the sensory supply to the tail region alone was left intact, a rhythmic response could be elicited (Fig. 11), though these preparations responded only by a single contraction to a nociceptive stimulus. The rhythm was normally slow, but the frequency could be increased to a certain extent by increasing the strength of stimulation (Fig. 11c). This rhythm was not sustained for any length of time, nor did it persist after stimulation. The range over which the strength of the stimulus could be varied was very limited; below that limit only a single response ensued, above it the fish curled round in a tonic contraction (Fig. 11e-g). At optimal strength 10-15 regular beats have been observed, both amplitude and frequency decreasing towards the end. After some minutes rest a similar response could be evoked.

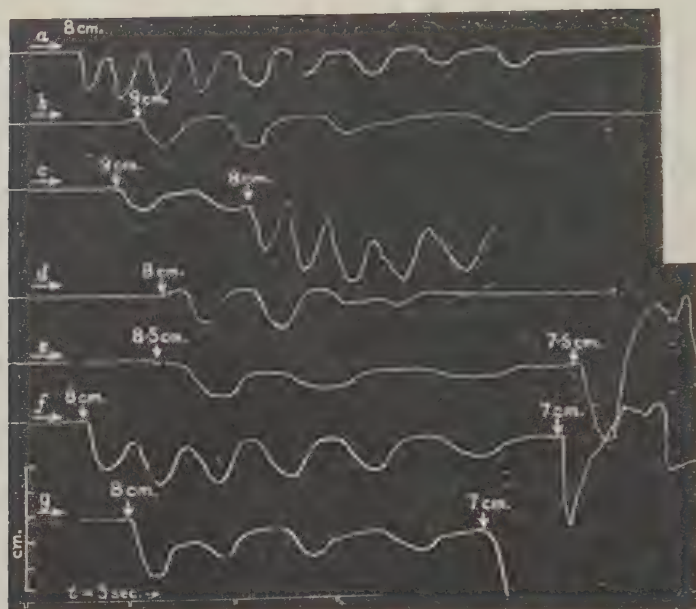


Fig. 11. Rhythmic response to continuous electrical stimulation applied to the posterior spinal cord of a spinal *Scyllium canicula*, completely de-afferentated except for the tail. The response is of limited duration and does not persist when stimulation is discontinued. Note (in c) that frequency and amplitude vary with the strength of stimulation. In e, f, g, a further increase in the strength causes the animal to curl round, bringing the head near the tail. The relative strength is indicated by the coil distance.

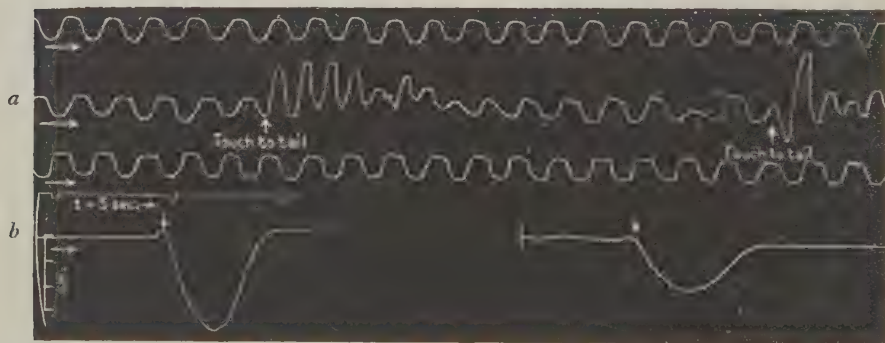


Fig. 12. (a) Persistent swimming rhythm of a spinal *Acanthias vulgaris* with its spinal cord entirely exposed. (b) The same preparation, completely de-afferentated, responding with a single contraction to electrical stimulation applied to the posterior spinal cord.

(5) So far I have not been able to obtain a rhythmic response in completely de-afferentated animals through the application of electrical stimuli to the cord. These attempts, however, were limited to one specimen of *Scyllium* and one of *Acanthias*; both responded with a single contraction despite considerable variation in the strength, frequency and site of application of the stimulus (Fig. 12).

DISCUSSION

Two opinions have been expressed as to the nature of the persistent swimming rhythm of the spinal dogfish.

Steiner (1885) thought that the cranial excitation, without which a teleost fish does not normally swim, is replaced in the spinal dogfish by the excitation arising from the cut surface of the spinal cord. As we now know, the spinal dogfish may survive for many weeks and still continue to swim; this view, therefore, has been generally abandoned.

The second theory, which has been widely accepted in recent years, conceives the neuro-muscular events which lead to locomotion in a fish as being originated by a spontaneous, automatic drive, emanating rhythmically from the central nervous system. It would be difficult to reconcile this picture with the results of the experiments reported above, for there can be little doubt that the persistence of the swimming movements is in full measure dependent on afferent excitation.

It is not hard to visualize afferent impulses being sent into the spinal cord, once the preparation has begun to swim, but little positive evidence can be advanced as to what causes the initial stroke in the majority of spinal dogfish. However, it is interesting to note that continuous sensory discharges have been recorded from nerves connected to unstimulated sense organs (Hoagland, 1933 *a, b*; Sand, 1937; Löwenstein & Sand, 1940); moreover, in skate and dogfish stretch receptors under constant tension have been observed to function continuously and rhythmically for more than an hour, and it was concluded 'that there is no limit to the duration of a discharge from a muscle under slight tension in the intact animal' (Fessard & Sand, 1937). These observations suggest that the first link in the chain which may be considered responsible for the apparent spontaneity of the swimming movements is represented either by such 'spontaneous discharges' in the sensory nerves, or by stimuli arising out of the environment. The evidence, therefore, is strongly in favour of a reflex nature of the locomotory rhythm, and does not support in any way the view of a spontaneous, automatic rhythm arising out of the central nervous system.

The external stimuli are, of course, only one link in the closed chain of events, and it is clear that central neurones enter into the process of maintenance of the swimming rhythm; they even may do so in a manner that differs from a linear reflex diagram. However, there does not appear to be any ground for the assumption that a process of central re-excitation, as it might arise from a 'self-exciting cycle' (Lorente de No, 1933, 1934; Young, 1936), is alone sufficient to perpetuate the movement. If that were the case, an extensively or completely de-afferentated

preparation might have been expected to continue its swimming movements after a brief releasing stimulus, of either exteroceptive nature, or after electrical stimulation applied to the cord.

The precise role of afferent excitation is a much-debated point in vertebrate physiology. While there can be little doubt that locomotory activity depends on afferent excitation, the question constantly arises whether the locomotory patterns depend on definite patterns of exteroceptive or proprioceptive stimuli, or whether they are determined by the architecture and physiology of the spinal cord.

The establishment of different reflex postures according to varying sites of stimulation make it reasonable to suppose that such postures depend on the activity of reflex arcs. These are obviously related to an external stimulus. However, the effect of this stimulus, which is conducted along established paths, partly leads through the central nervous system, and thereby introduces central properties into this reaction. One of these is reciprocal excitation-inhibition. When after spinal transection only diffuse stimuli are sent into the cord, the result is, nevertheless, an undulatory posture. From this we must conclude that the spinal cord responds as one unit.

However, the establishment of the locomotory posture is only one of the problems of animal locomotion; the other concerns the mechanism of its continuous movement along the body. The tendency to form static reflex postures after extensive de-afferentation—also noted by v. Holst (1935) in the de-afferentated tench—points to a reflex nature of the dynamic properties of such postures in intact animals. The mechanism might be imagined to operate as follows: An external stimulus throws the body of the dogfish into a characteristic S-shape. In the next instant this reflex posture integrates with its own proprioceptive reflexes which may cause a dislocation of the posture along the body, and so on. If the initial reflex posture fails to evoke proprioceptive reflexes it can be expected to remain stationary. So far an experiment, comparable to Graham Brown's (1912 *a, b*) de-afferentated mammalian preparation, responding rhythmically to continuous spinal cord stimulation is still lacking in fish or other vertebrate animals. Unless it is supplied, it appears premature to accept the view that the propagation of the locomotory wave along the body can be accomplished by a purely central mechanism. The fact that in de-afferentated preparations afferent excitation may be replaced by artificial stimuli applied to the cord may show that the cord can act as an oscillator, but the substitution of one type of stimulation with another type does not provide evidence for a central drive, while it has never been seriously doubted that the property of reciprocal excitation-inhibition is located in the central nervous system. On the other hand, it may be significant that after extensive de-afferentation only one type of rhythmic response has been obtained through electrical stimulation of the cord, whereas the intact animal exhibited two types. If future work should produce evidence for the view that the slow rhythm of wide amplitude thus obtained is comparable to the rhythm of a fish under external restraint or pressure—a condition which might prevail on emergence of early vertebrates from water to land—this rhythm might be more closely related to ambulatory function than to swimming.

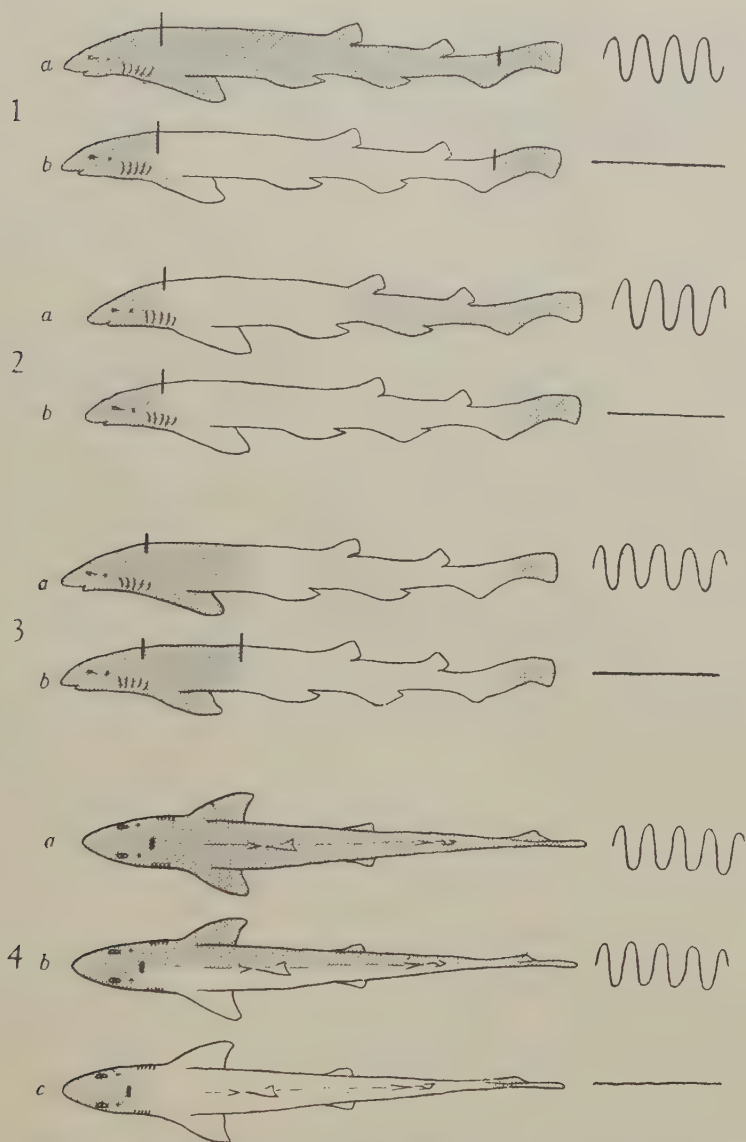


Fig. 13. The effect of de-afferentation upon the locomotory rhythm of the spinal dogfish. The white regions represent the desensitized areas of the body. The level of spinal transection is indicated by a thick line. ~~~~ = rhythm; — = inactivity. 1 (a) Persistent rhythm of a spinal *Scyllium canicula*. (b) The rhythm is abolished after de-afferentation. 2 (a) Persistent rhythm of an anteriorly de-afferented *Scyllium*. (b) Disappearance of the rhythm after complete de-afferentation except for the tail. 3 (a) Rhythm after de-afferentation of the posterior body region. (b) After transection of the cord at the level of de-afferentation the de-afferented zone becomes silent. 4 (a) Persistent rhythm of a *Acanthus vulgaris*. (b) The rhythm does not appear modified after complete unilateral de-afferentation. (c) Bilateral de-afferentation abolishes the rhythm.

SUMMARY

Some of the more striking effects of de-afferentation in the spinal dogfish are diagrammatically represented in Fig. 13.

1. The persistent locomotory rhythm of a spinal dogfish depends upon afferent excitation. If all afferent excitation is cut off by severance of all dorsal roots, the rhythm is abolished (Fig. 13, 1).

2. The rhythm clearly emerges when about half the number of all the dorsal roots is transected, irrespective whether the anterior or the posterior half of the animal be de-afferentated (Fig. 13, 2 and 3), or whether complete unilateral de-afferentation is executed (Fig. 13, 4).

3. Extensively de-afferentated preparations may exhibit swimming movements after exteroceptive stimulation. These swimming movements do not persist.

4. Preparations de-afferentated except for the tail exhibit after exteroceptive stimulation a static reflex posture.

5. The de-afferentated musculature takes part in both tonic and rhythmic responses as long as it is connected through the spinal cord with normally innervated musculature.

6. In response to electrical stimulation applied to the cord of a spinal dogfish two distinct types of rhythmic response have been evoked.

7. No rhythmic responses have been obtained through electrical stimulation of the spinal cord in completely de-afferentated preparations.

8. No evidence has been found in support of the view that the swimming rhythm emanates through a spontaneous, automatic activity from the central nervous system.

The author wishes to repeat the acknowledgements and sincere thanks expressed in the preceding paper.

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THE MECHANICS OF AMPHIBIAN LOCOMOTION

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(With Sixteen Text-figures)

I. INTRODUCTION

Apart from the classical studies of Borelli (1680) and Weber & Weber (1836) very little work was done on the mechanical aspects of animal locomotion until the advent of photography, but starting with Stillman (1882), Marey (1895) and Muybridge (1899), who all played a considerable part in the development of cine-photography, extensive studies were carried out by analysis of photographic records. The most notable example was the very elaborate and complete study of human walking by Braune & Fischer (1895) and Fischer (1899, 1901 *a, b*, 1904 *a, b*); similar work has since been done by Fenn (1929, 1930 *a, b*) and Elftman (1939 *b*, 1940, 1941) on man, and Hirsch (1931) on the frog's jump. The estimation of forces from photographic records involves large possible errors, and attempts have therefore been made to approach the problem by means of direct measurement of the forces exerted on the ground. Much of the early work in this field is reviewed by Elftman (1934). Other types of apparatus were used by Marey (1873), Amar (1916), Fenn (1930 *a, b*) and Gray & Lissmann (1938). Finally, Elftman (1938, 1939 *a, b* and *c*) invented an apparatus which would record simultaneously the forces exerted on the ground along three orthogonal axes as well as the position of the centre of pressure of the foot in man. Manter (1938) employed a modified form of this apparatus for studies on the cat. Manter's apparatus consisted essentially of a movable platform let into a fixed stage and supported at the four corners on spiral springs. He retained only those records in which the feet had been placed approximately centrally on the platform. Such an apparatus cannot eliminate horizontal rotation of the platform or tilting, both of which introduce errors into the force records, and although such movements may have been small in the cat, the rotary forces about the long axes of the limbs have only been measured in man (Elftman, 1939 *b*), and these, together with the tilt, might cause serious inaccuracy in some animals. In addition, if such an apparatus were to be adapted for use with very small animals these errors would be relatively increased and especially so in animals with a large plantar surface over which the centre of pressure moves during the stride (e.g. toad hindfoot). Up to the present, therefore, no type of apparatus has been produced suitable for the accurate measurement of the forces exerted on the ground by such small animals as the living Amphibia.

Although the records of the forces exerted on the ground provide a valuable method of analysis of the forces acting on the body as a whole, they have not generally

been recorded in a form which makes possible any analysis of the internal mechanics of the limbs and body. Wermel (1934, 1935) and Stewart (1937, 1939) studied this aspect of the subject by means of operations on bones and muscles, and there has been a good deal of work on the relation between the fine structure of bone and cartilage and the mechanical stresses and strains to which they are subjected (reviewed by Murray, 1936). Studies on the internal mechanics of the limbs and body have been largely confined, however, to purely theoretical deductions based on the anatomy and type of movement executed in living animals (see reviews by Steindler, 1935; Böker, 1935; and Nauck, 1938) and a considerable amount of similar theoretical work on extinct animals (notably by Watson, 1917, 1926; Gregory, 1912, 1915, 1928; Gregory & Camp, 1918; Gregory & Raven, 1941; Romer, 1922; Romer & Byrne, 1931; Romer & Price, 1940; Schaeffer, 1941; Westoll, 1943; and White 1939). Unfortunately, there has been very little correlation between studies on living and extinct forms.

Recently, however, Gray (1944) has carried out a far more complete theoretical analysis of the internal mechanics of the tetrapod skeleton and has clarified the type of experimental data required to investigate the subject. The most fruitful line of approach appears to be a combination of photographic analysis with accurate records of the forces exerted on the ground, and a full comparative study of this type on different tetrapods is needed. By such a study it should be possible both to improve our knowledge of the general mechanical principles of tetrapod locomotion and also to elucidate the internal mechanics and functional morphology of the living animals investigated, thereby supplying a more exact basis for work on extinct animals. The present paper describes experimental work carried out on the Amphibia as the first stage of a comparative study. The species principally used were the common toad, *Bufo bufo*, and the crested newt, *Triturus cristatus*, but the natterjack toad, *Bufo calamita*, the common frog, *Rana temporaria*, and the smooth newt, *Triturus vulgaris*, were also used for comparison. The first two species are referred to in this paper as the 'toad' and 'newt' respectively.

II. METHODS

In order to record the forces exerted on the ground an entirely new type of apparatus was used. A movable platform is supported on two horizontal strips of steel clock-spring, which are set vertically on edge (Fig. 1*a*); these are soldered at one end to a metal base and supported at the other end by a bow of similar steel spring. Such a mechanism allows movement only along one horizontal axis (*EF* in Fig. 1*a*), and no rotation in the horizontal plane or tilt are possible. This unit was mounted on a second similar unit allowing movement along a horizontal axis at right angles to the first, and this in turn on a third slightly different unit allowing vertical movement only. The apparatus as ultimately employed is shown in Fig. 1*b*. The movable platform *ABCD* was let into a fixed stage along which the animal walked. The forces in the three axes were recorded by means of three straw levers, writing side by side on a smoked drum and attached to the apparatus by means of bearings of the

type shown in Fig. 1*c*. The whole movable part of the apparatus was made as light as possible in order to reduce the period of oscillation, and was damped sub-critically by means of an aluminium vane in an oil-bath (attached at *F* in Fig. 1*b*). The damped period was about $\frac{1}{25}$ sec. for the horizontal units and rather more for the vertical unit. The whole apparatus was filmed from above, using an inclined mirror to give synchronous dorsal and lateral views of the animal, with the levers arranged so as to write in the same photographic plane; by this means a simple synchronization was effected between the force records and the exact positions of

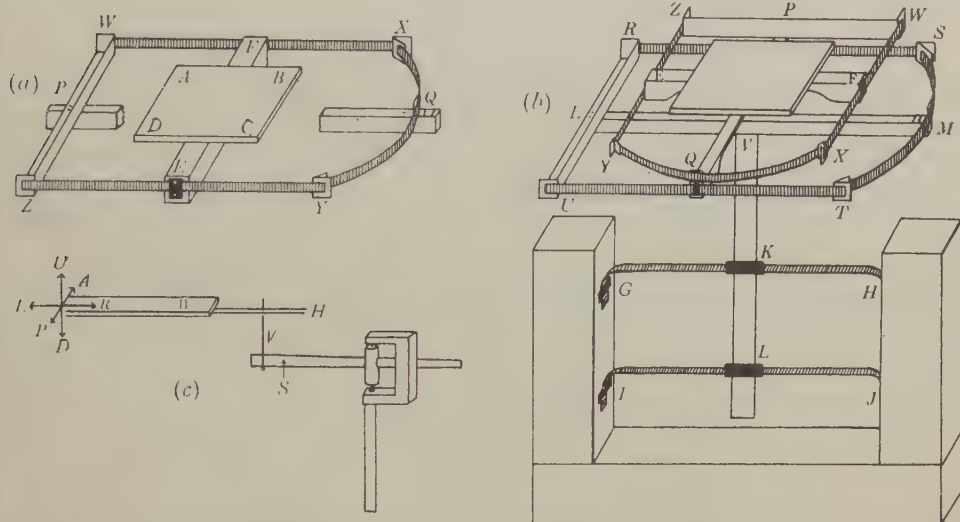


Fig. 1. The apparatus for recording the forces exerted on the ground. (a) The type of unit employed for measuring the horizontal forces. The platform *ABCD* is supported on the wooden bar *EF* which is supported by two strips of spring *WX* and *YZ*. These are soldered to a metal frame at *W* and *Z*, and at *X* and *Y* are soldered to a bow of similar spring *XY* held under tension by the bar *PQ*. Movement is possible only along the axis *EF*. (b) The apparatus as employed. The top unit is identical to (a). The bar *PQ* is supported by a similar pair of springs *RS* and *TU*, which are held by the bar *LM*. This is supported at *V* by a vertical rod fixed at *K* and *L* to a third pair of springs *GH* and *IJ* set horizontally. The ends of these two springs are bent over into the vertical plane and screwed down to a wooden frame so that vertical movement only is allowed to the rod *VKL*. (c) The type of bearing used to attach the levers to the apparatus. The bar *W*, attached to the platform, moves in all three axes, but the two horizontal pins *H* fit exactly on to a vertical pin *V* so that only movement in the axis *AP* is transmitted to the straw *S* to which *V* is attached. A constant lever arm is also maintained in all positions of the platform. Similar bearings were used for all three axes.

the limbs. The force records were accurate to the nearest $\frac{1}{4}$ g. in the horizontal axes and to the nearest g. in the vertical axis; the actual movements of the platform were normally never more than $\frac{3}{4}$ mm. in each direction. Forces of rotation about the long axis of the limb could not affect the system, and since tilt was also eliminated it made no difference where the centre of pressure lay on the surface of the foot or where the foot was placed on the platform. The animals were induced to walk along the stage by mechanical stimulation and by placing a dark box in front of them and the photographic lamps behind.

Of a variety of operational techniques used for paralysing muscles the most satisfactory was found to be the removal of a length of nerve of about 2 mm. Skin wounds had no apparent effect on the gait, and most experiments were carried out about a week after operation. In order to measure the rotation of the limb bones, pins were inserted into them in previously drilled holes. The rotation was measured from simultaneous dorsal and lateral photographs by the use of a solid model which could be moved into the positions shown. Some indirect cine-X-ray photographs giving dorsal views of toads in movement were taken on Prof. A. E. Barclay's apparatus (Barclay, Franklyn & Prichard, 1940).

III. FORCES ACTING ON THE BODY AS A WHOLE

In normal walking the Amphibia show the diagonal pattern of limb movement discussed by Gray (1944). For the purposes of the present study the stride was divided up into phases as shown in Fig. 2 for the toad. Phases 0-6 constitute a complete locomotory cycle (one stride = two steps; following Muybridge, 1899), but, since the force records were obtained first from a forelimb and then from the ipsilateral hindlimb in each case, each record covered a period of $1\frac{1}{2}$ strides (Fig. 2, phases 0-9). These phases supply a scale of relative time which is unaffected by the speed of movement of the animal and makes possible a comparison of different strides and different animals. The newt stride can be divided up into similar phases. The body of the toad is held clear of the ground in normal walking and, statements to the contrary notwithstanding, when walking on a dry surface the British newts rarely drag their bodies along the ground except momentarily when movement is slow; in fast walking the tail only drags and the body is normally supported for a short time in each stride on two diagonally opposite feet only. This type of locomotion appears to be general amongst the terrestrial and semi-terrestrial urodeles.

The definitions adopted by Gray (1944) for the limb movements in mammals are not strictly applicable to Amphibia and reptiles, and the following modified definitions, which apply equally to all groups of tetrapods except man, are therefore employed in the present paper. *Protraction* and *retraction* of the humerus and femur are movements causing the distal ends of these bones to move respectively forwards and backwards longitudinally. *Adduction* and *abduction* of the humerus and femur are movements causing the distal ends of these bones to be brought respectively nearer to and farther from the ventral median line. The term *rotation* is used in the case of the humerus and femur only for rotation about their own long axes and is described as clockwise and anticlockwise as seen from the right side of the animal.

Gray discussed the mechanics of the standing of tetrapods and the conditions necessary for equilibrium in terms of the forces exerted at the feet. In a moving animal when periods of instability with respect to any of these forces are introduced we should expect the acceleration of the centre of gravity of the body in the appropriate direction to be proportional to the corresponding unbalanced force, and records of these forces should therefore correspond to the acceleration of the centre of gravity measured by photographic analysis. It may also be noted that a pattern of external forces acting on an animal which would cause instability and collapse

if the animal were stationary (*static instability*) may in a moving animal be essential to prevent collapse, owing to the momentum which the body already possesses, and

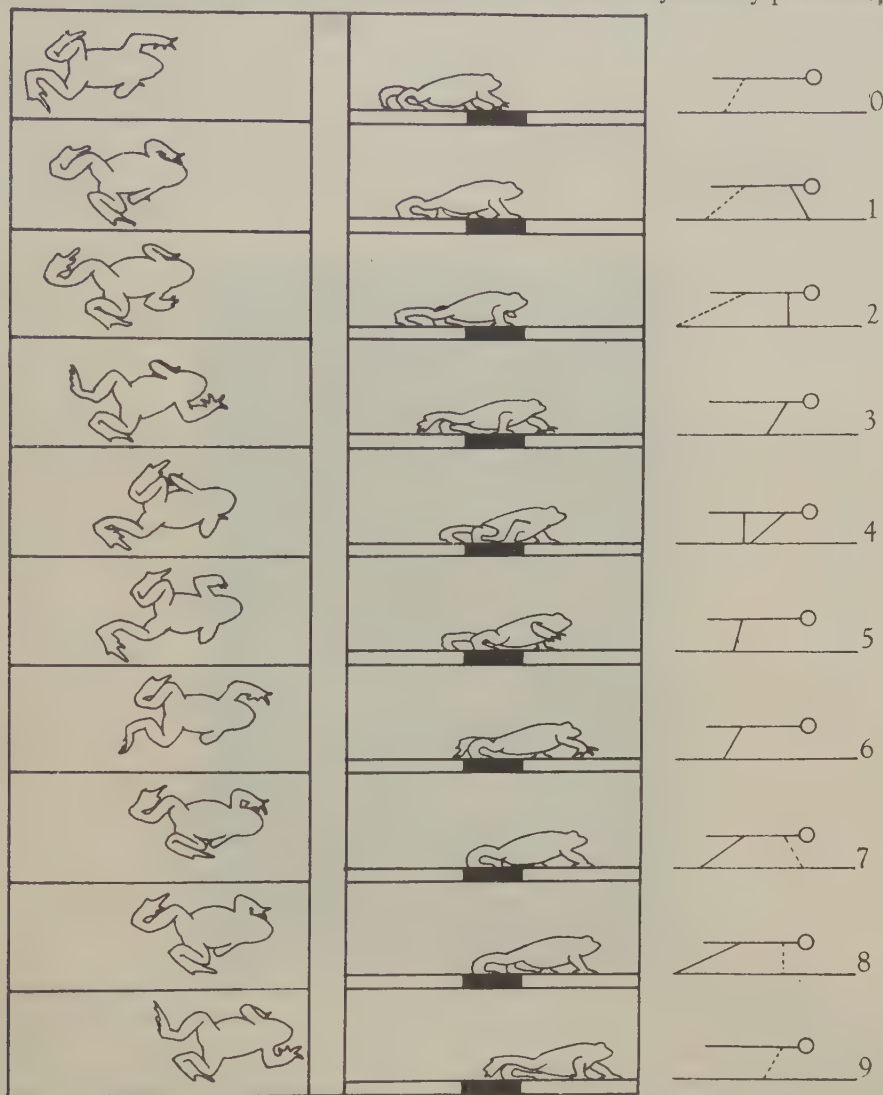


Fig. 2. Synchronous dorsal and lateral views of the normal walking of a toad. The numerals indicate the phases of the stride employed as a relative time scale. Phases 0-6 constitute a complete stride and phases 0, 3, 6 and 9 are corresponding stages of different steps (the photograph for phase 0 is a little early as the right hindfoot is not yet off the ground). The symbols represent the relation of the left limbs to the recording platform, marked in the side view by the black bar. The limbs shown in the symbols by a full line are on the platform, those by a broken line are off it. Since the side view was obtained from a mirror the near limbs are those of the left side. The left forefoot first carries the weight about midway between phases 0 and 1; * the left hindlimb is lifted off the ground between phases 8 and 9. The limbs of the right side do not touch the recording platform, which is on the left of the stage.

* Events occurring between successive phases are indicated elsewhere in this paper by adding the fraction $\frac{1}{2}$ to the earlier of the two relevant phases.

so bring about what can be termed a *dynamic stability*. For the same reason an animal in movement can assume postures which would be statically unstable and could never be assumed in standing, but are dynamically stable due to the momentum of the body.

The toad

All the toads used of both sexes gave force records of the same basic type. Fig. 3 shows a typical trace, and this pattern of forces was very constant when plotted against the scale of relative time supplied by the phases (Fig. 2). Since the tips of the toes of the hindfoot are placed on the ground about level with the middle of

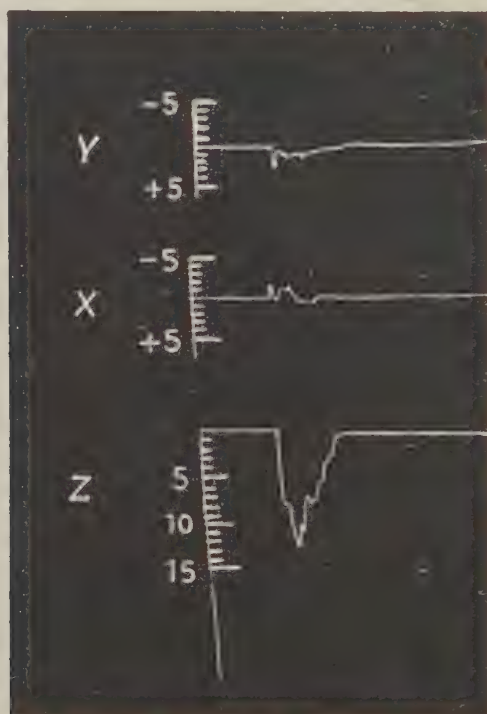


Fig. 3. A typical trace from the smoke drum of a toad weighing 20.8 g. Y, forces transverse; plus, lateral; minus, medial. X, forces longitudinal; plus, propulsive; minus, retarding. Z, forces vertical. Calibration in grams. The record reads from left to right.

the forefoot it is not normally possible to separate the forces acting on the fore- and hindfeet about phase 4. A record in which this was possible, however, is given in Fig. 4. The apparatus only recorded the forces acting on one foot at a time, except in phase 4, but as the pattern was so regular it was possible to estimate the forces acting on each foot in every position and so, from the record of the forces on one side, together with the photographs of the positions of the limbs, to calculate the total forces acting on the body in each of the three axes. The vertical forces are shown in Fig. 5 and the horizontal forces in Figs. 6 and 7. The total force curves so obtained cannot be considered to be very accurate but give a general picture of the forces which corresponds very well with the approximate acceleration

curves of the centre of gravity calculated from the photographs. These acceleration curves were obtained from the movement of a fixed point on the body close to the centre of gravity, but since a large part (nearly half) of the toad's mass lies in the legs the centre of gravity moves a certain amount during the stride and the resulting curves are therefore not very accurate either, but the general correspondence of the

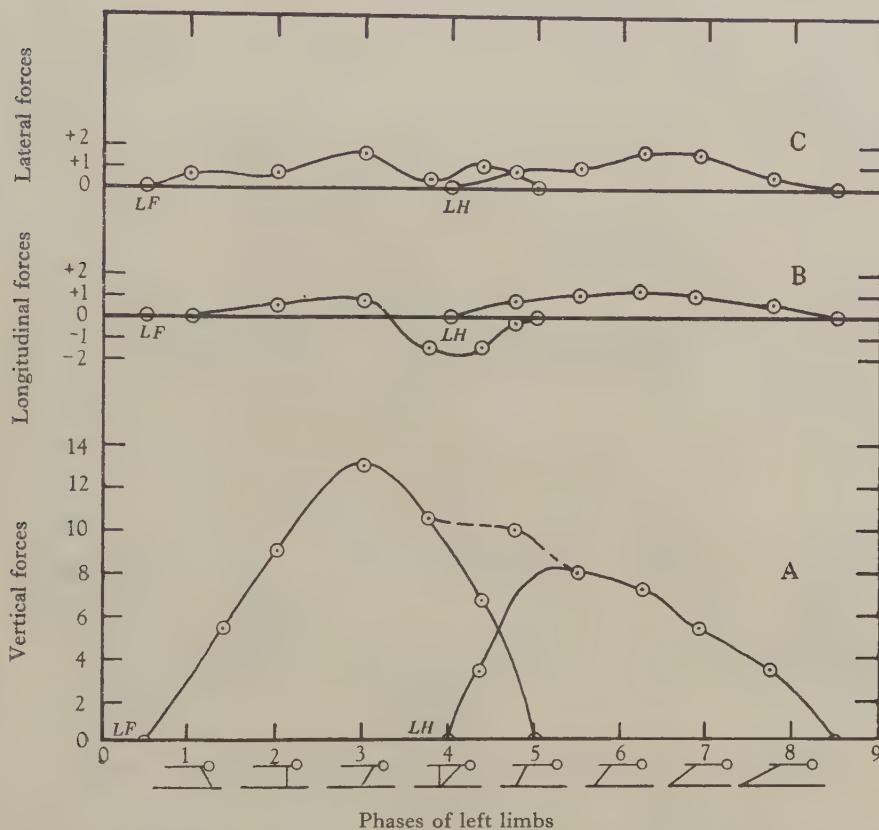


Fig. 4. A record of the forces in the three axes in a toad weighing 20.8 g. during a stride in which it was possible to separate the forces acting on the fore- and hindfeet in phase 4. All forces in grams. Longitudinal forces: plus, propulsive; minus, retarding; transverse forces: plus, lateral. The dotted region of the curve for vertical forces represents the sum of the vertical forces on the fore- and hindfeet of the left side. A, vertical forces. B, longitudinal forces. C, transverse forces. *LF* and *LH* are the points at which the left fore- and left hindfeet respectively were placed on the ground. The symbols for the phases of the limbs show only the limbs which are on the recording platform (see Fig. 2).

maxima and minima of the two curves is significant. The distribution of the weight between the two sides of the body and the moments of rotation of the body about the longitudinal, transverse and vertical axes also correspond generally in their maxima and minima to the observed accelerations (Fig. 8). All these facts confirm Gray's analysis of the mechanics of the tetrapod skeleton; in so far as the animal departs from his conditions of equilibrium the expected type of accelerations occur.

Gray points out that stability with respect to vertical forces is normally dependent not only on the total vertical reaction at the feet being equal to the weight, but also on having at least three feet on the ground with the centre of gravity lying within the triangle of support. He demonstrated that this latter condition can only

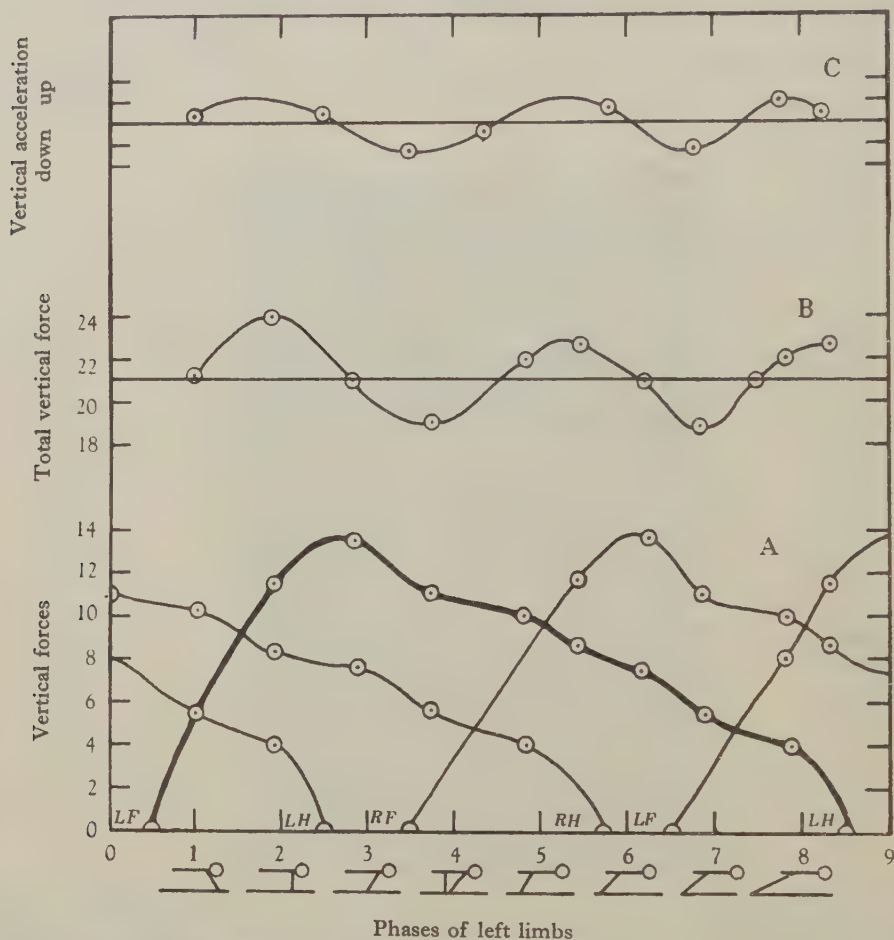


Fig. 5. Vertical forces acting on all the feet of a toad weighing 20.8 g. Forces in A and B in grams. Acceleration in C in arbitrary units. A. Forces acting on each of the feet. The thick line is the actual force record, the others being calculated from this and the positions of the limbs. LF, RF, points at which the left forefeet and the right forefeet are first placed on the ground. LH, RH, points at which the left hindfeet and right hindfeet are lifted off the ground. B. Total vertical force acting on the body calculated by addition of those in A. The base-line is the weight of the toad. C. The vertical acceleration of the centre of gravity of the body during the same stride as calculated from photographs showing the movements of a fixed point on the body near to the position of the centre of gravity. The same stride as Figs. 6 and 7.

be maintained by means of a diagonal pattern of limb movements such as is found in the slow walking of most tetrapods. To these conclusions of Gray's it may be added that if the diagonal pattern is present there will always be a short period, during the transfer of the weight from one triangle of support to another, when the

centre of gravity lies on the line joining the centres of pressure of two diagonally opposite feet, and the animal could then be statically stable with respect to vertical forces even if only these two feet were on the ground. Normally such a period of stability would be only momentary, but if the centres of pressure were to move forwards over the surface of the feet its duration could be of appreciable length.

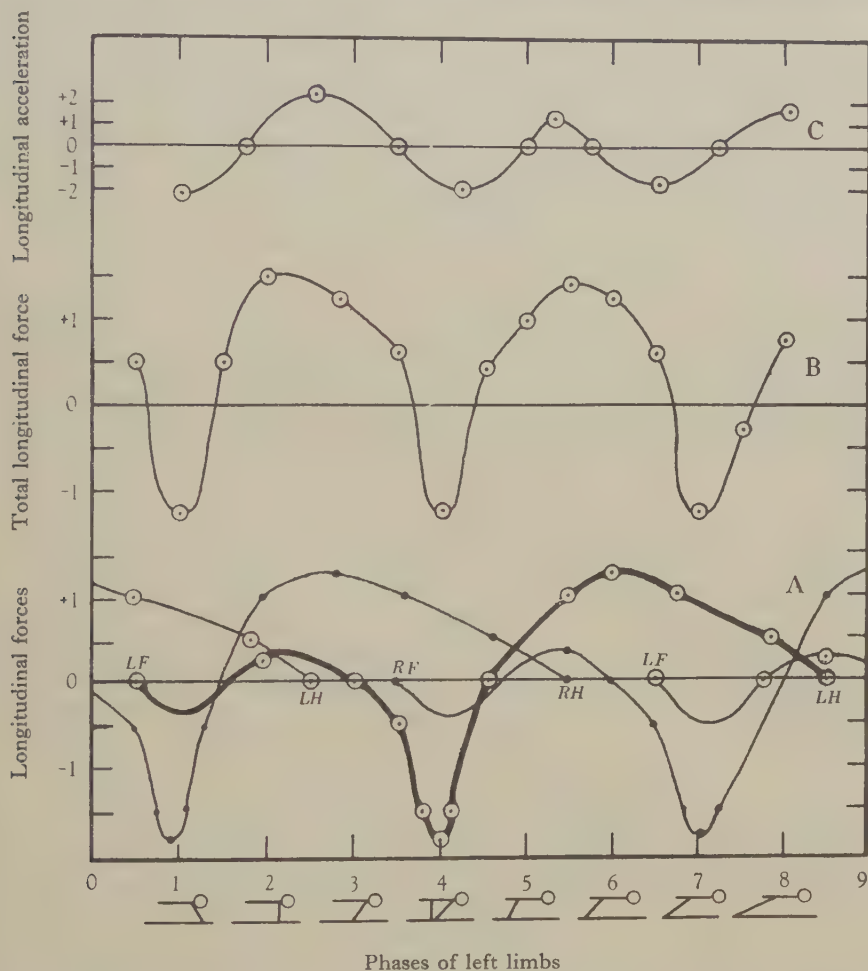


Fig. 6. Longitudinal forces acting on all the feet of a toad weighing 20.8 g. Units and symbols as in Fig. 5. The same stride as Figs. 5 and 7. Plus, accelerating forces; minus, retarding forces. A. Longitudinal forces on the four feet. B. Total longitudinal force. C. Acceleration in the longitudinal axis measured from the photographs.

Static instability with respect to vertical forces (and similar considerations apply to horizontal forces) can therefore be of two kinds. Instability due to the vertical reaction at the feet not being equal to the weight may be termed *vertical rectilinear instability*. Instability due to lack of balance of the vertical moments may be termed *vertical rotational instability*.

The periods during which the feet are in contact with the ground were recorded photographically for slow, medium and fast walking of the toad, and it was found that, whereas in slow walking there are always at least three feet on the ground and the animal is probably always approximately in a state of vertical rotational stability, as the speed of forwards movement increases, progressively longer periods with

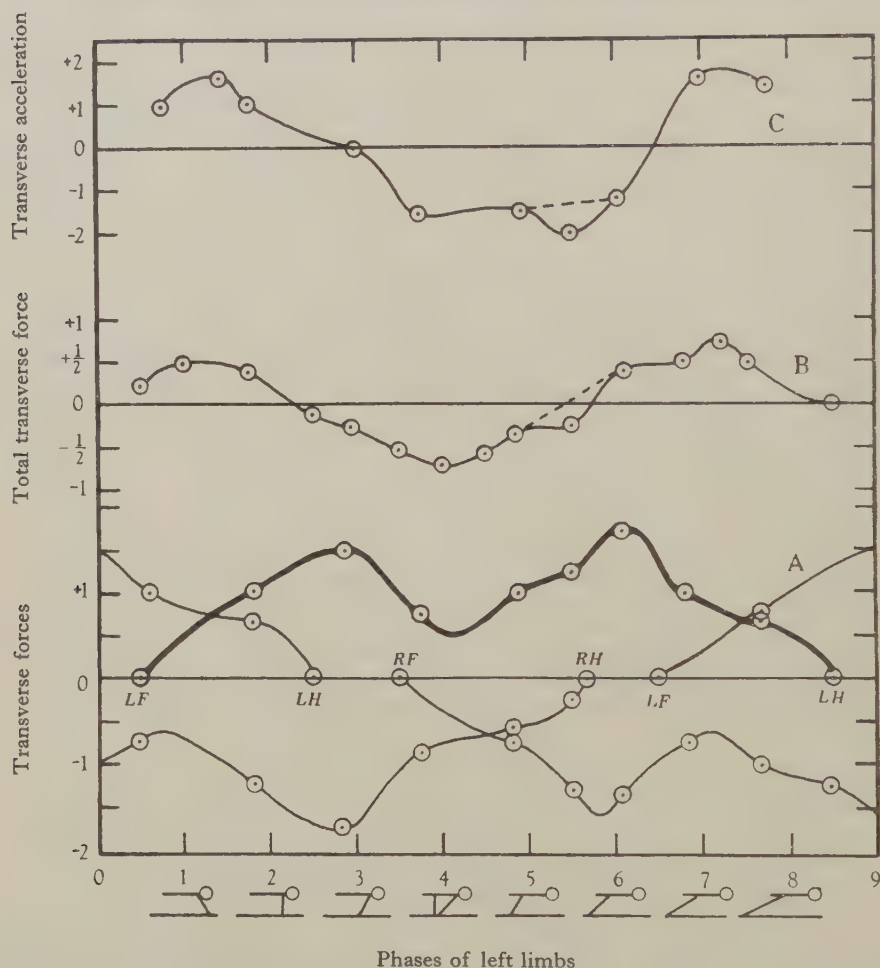


Fig. 7. Transverse forces acting on all the feet of a toad weighing 20.8 g. Units and symbols as in Figs. 5 and 6; record for same stride as those figures. Plus, forces to left; minus, forces to right. The reading at phase 5.4 is probably due to an irregularity in the stride, and the normal curve would probably follow the course of the dotted line.

only two feet on the ground are introduced, and in fast walking these must represent periods of static instability with respect to vertical rotational forces.

A detailed analysis of the mechanics of the toads' walk from the force records and photographs explains how these periods of static instability are overcome. Fig. 9 shows outlines of consecutive frames of a film of a toad walking rapidly.

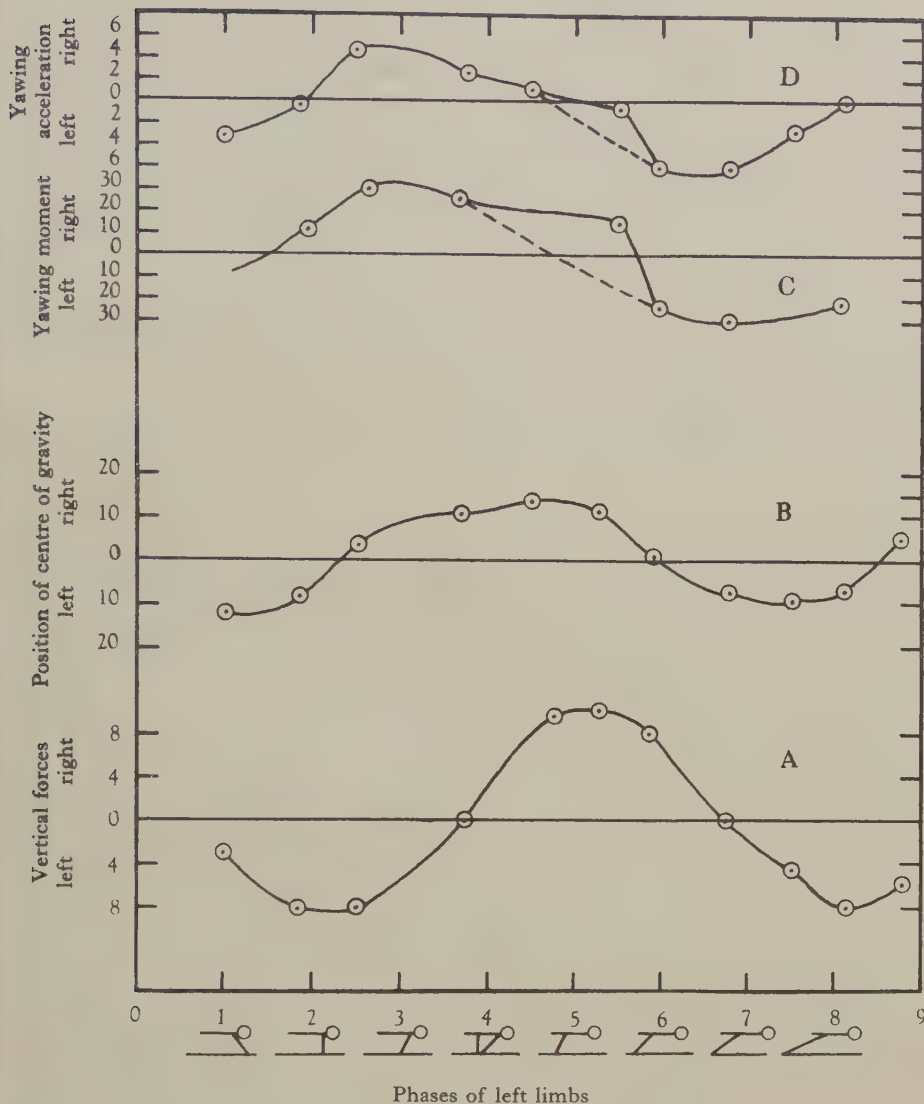


Fig. 8. Correspondence of force records and movements of the body of a toad weighing 35.0 g. A. Distribution of the weight between the two sides of the body in a toad. Calculated from a figure similar to Fig. 5 A. Excess weight on each side over that on the other in grams. B. Lateral movements of the centre of gravity of the body calculated from the movements of a fixed point near to the centre of gravity. Arbitrary units. Same stride as A. As the centre of gravity moves over to one side so the proportion of the weight on the limbs of that side of the body is increased. C. Yawing moments calculated from the force records as in Fig. 7 A and the corresponding photographs. Arbitrary units. Left and right refer to the tendency to swing the head to the left and right. D. Acceleration of yawing movements calculated from the photographs of the same stride as A, B and C. Arbitrary units. The reading at phase $5\frac{1}{2}$ in C and D is probably due to an irregularity in the stride, and the normal curve would probably follow the course of the dotted line. There is a marked general correspondence between C and D which includes the irregularity at phase $5\frac{1}{2}$. A similar general correspondence was found between the pitching moments and accelerations and also between the rolling moments and accelerations.

The centre of gravity is represented by a fixed point just behind the sacrum. In Fig. 9 (1) the centre of gravity lies within the triangle of support and the animal could be stable in this position, but from Figs. 5 and 6 it is clear that at this stage (phase 2) the total vertical force is greater than the weight and the total forward velocity is at a maximum so that the centre of gravity will be accelerated upwards and forwards. It can also be shown (see Fig. 8 note) that there is at this stage a considerable pitching moment tending to raise the back end of the body and to lower the head. All these features can be explained in terms of an excess vertical and propulsive force at the hindfoot A. In Fig. 9(2) (phase 2½) only two feet are bearing the weight and the upwards and forwards accelerations of the centre of gravity and the pitching moment are reduced, also the centre of gravity is behind the diagonal support so that the animal is statically unstable, but owing to the upwards and forwards momentum imparted to the centre of gravity in phase 2 the animal does not collapse (i.e. it is dynamically stable). Between Fig. 9(2)

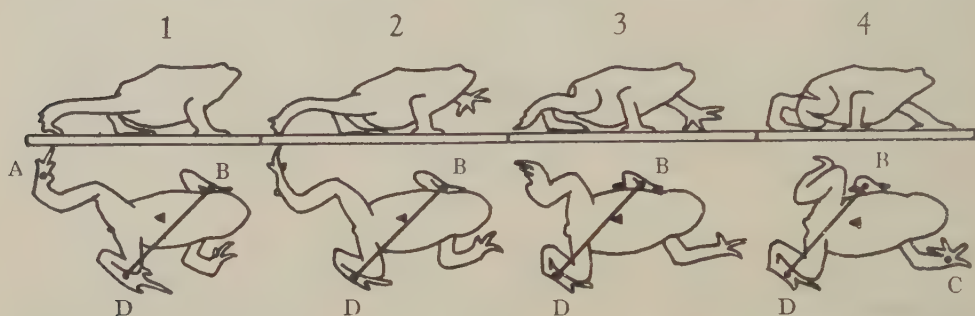


Fig. 9. Outlines of four successive frames of a toad in normal fast walking, showing the support of the body at different stages of the stride. The side views are mirror views corresponding to the dorsal views. The black triangle represents the position of the centre of gravity of the body; the black circles on the feet represent stages in which they are bearing some of the weight. The centres of pressure of the feet B and D are joined by a line. Explanation in text.

and Fig. 9(3) there must be a momentary period of static rotational stability when the centre of gravity lies vertically over the diagonal support, but in Fig. 9(3) (phase 3) the centre of gravity is in front of the diagonal support and the animal is again in a state of static rotational instability. During this period the total vertical reaction falls below the weight so that the centre of gravity is accelerated downwards, but since it has a considerable upwards velocity imparted to it in the previous phase it does not start to fall vertically until just before phase 3½ (Fig. 9(4)). When the other forefoot C is placed on the ground, a triangle of support is restored and the negative acceleration gradually reduced. Since the centre of gravity is at a maximum height above the ground at this stage it can be allowed to drop a certain amount without the body touching the ground. At the same time the longitudinal acceleration falls off gradually and is then suddenly reversed when the foot C is placed on the ground (Fig. 6). The pitching moments are also such that up to this point the head is lowered progressively and, afterwards, raised.

The general picture is of a ricochet movement of the centre of gravity which is projected upwards and forwards at the start of the period of static instability and

brought back again to the original level by the braking and supporting action of the protracted forelimb when the latter is placed on the ground. The periods of static instability are therefore dynamically stabilised by a process which necessitates considerable fluctuations in the forces exerted on the ground. Such dynamic stability involves an expenditure of energy appreciably greater than that needed to maintain progression of the truly static type seen when a toad is walking slowly. This wastage of energy is discussed below.

The newt

Newts were found to be far less easy to handle during these experiments, and owing to their small size the records obtained were relatively less accurate. Nevertheless, a number of good records all showed the same general pattern of forces. The relatively large pitching and rolling movements, together with the lateral flexure of the body, made it impossible to fix the position of the centre of gravity at all accurately, and no curves for the acceleration could therefore be obtained from the photographs. The shifting of the weight from side to side and from fore- to hind-limbs, however, followed a pattern very similar to that in the toad. Since the movements executed are in general outline very similar also, it is probably safe to assume that the statics and dynamics of the two forms are in principle the same.

IV. PERIODS OF STATIC INSTABILITY WITH RESPECT TO VERTICAL FORCES

As the speed of forward movement increases the toad shows increasingly long periods of static instability with respect to vertical forces. Marey (1873) gives figures which show that the same is true for man and the horse: as the speed of forward movement of a horse increases, periods occur when only two, one and finally no feet are in contact with the ground. Observations confirm that this is true also for the cat and dog and a number of other animals. It seems probable that it is a general rule. Although such periods of static instability with respect to vertical forces necessitate apparently wasteful expenditure of energy, the following considerations must be borne in mind.

The length of the stride of an animal is determined by three factors: the length of the limbs, the angle of swing of the limbs and the distance through which the proximal articulation of the limb moves during the period in which the foot is not in contact with the ground (i.e. protraction phase). The term 'acceleration increment', which was employed by Gregory (1912) in a rather ill-defined sense, may be used to describe this third factor. Of the three factors, the first is constant in any animal and the second varies only within small limits as a rule, but the third is capable of very considerable variation. In an animal which always has at least three feet on the ground the acceleration increment cannot be increased above a certain very small magnitude, but if a period with only two feet on the ground is introduced it can be greatly increased, while periods with only one and with no feet on the ground make possible still further increases. The introduction of these periods with less than three feet on the ground, therefore, makes possible an increase

in the length on the stride. This in turn makes possible a decrease in the frequency of the oscillation of the limbs. This will involve a considerable reduction in the energy expended in moving the limbs, especially at higher speeds, because the energy required to stretch and contract the muscles against their own viscosity is greatly increased as the speed of these actions is increased.

Periods of static instability, therefore, permit a considerable saving of energy in movements of the limbs, although they necessitate a larger expenditure of energy in maintaining non-essential fluctuations of the total external forces acting on the body. It is probable that the latter is less than the former at higher speeds, owing to muscle viscosity, so that these periods of static instability with respect to vertical forces make possible a saving of the total energy expended in rapid locomotion and therefore facilitate higher speeds of progression.

V. THE PATTERN OF EXTRINSIC MUSCLE COUPLES

Gray (1944) has shown that the limb musculature of a tetrapod may be divided functionally into *intrinsic* muscles, having their origin and insertion both on the limb segments, and *extrinsic* muscles, having their origin on the body and insertion on the limb. He has also shown that the forces exerted by a limb on the body and ground may be divided into: (1) the forces due to its function as a *strut*, which are dependent on the angle of inclination of the limb and its axial thrust (due to the activity of the intrinsic muscles); and (2) the forces due to its function as a *lever*, which depend on the angle of inclination of the limb and the activity of the extrinsic muscles.

The horizontal forces exerted on the ground by the limbs owing to their action as struts may be termed the *horizontal strut effect* and can be calculated from the angle of inclination of the limb and the vertical force acting at the foot in that position (see Gray, 1944, p. 98). The horizontal forces due to the action of the limbs as levers may be termed the *horizontal lever effect* and can be calculated from the horizontal strut effect if the actual horizontal force is known; the horizontal lever effect is the difference between the horizontal strut effect and the actual horizontal force. From the records of the forces exerted on the ground at the feet and synchronous photographs of the limb positions it is therefore possible to calculate the horizontal lever effect and hence to ascertain which group of extrinsic muscles is exerting the greater couple on the limb at any stage. For these purposes it is convenient, and Gray has shown that it is legitimate, to separate the forces in the transverse and longitudinal axes and deal with them independently.

Apart from the present study the only data available for such calculations are Manter's (1938) for the cat (although his force records and outlines of the limb positions only correspond for a single stride) and Elftman's (1940) for man. In the present study, however, a very constant pattern of activity was found in the toad (Fig. 10). While the forefoot is in front of the shoulder joint a retractor couple acts on the forelimb; when the foot is behind the shoulder joint a protractor couple operates. The centre of pressure of the hindfoot is normally never in front of the acetabulum in the toad (this is most clearly seen in cine-X-ray photographs), and

the hindlimb muscles exert a protractor couple throughout the stride. It is probable that the antagonistic muscles are always exerting some tension and that the tension in both groups may be quite high when the change-over occurs from a retractor to

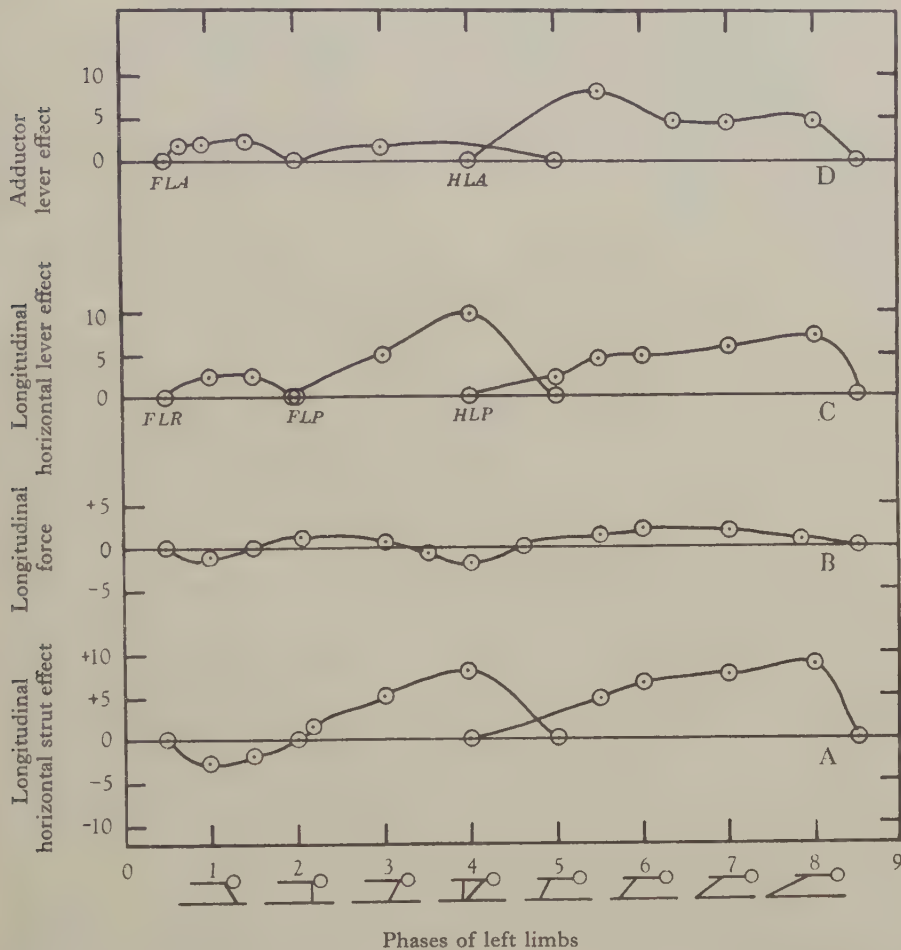


Fig. 10. The muscle couples acting on the limbs of a toad. The same toad as Figs. 5, 6 and 7. Forces on the fore- and hindlimbs separated. A. Longitudinal horizontal strut effects calculated from the vertical forces and the limb positions. B. Actual longitudinal horizontal forces from the corresponding force record. Forces in A and B in grams. Plus, accelerating forces; minus, retarding forces. C. The longitudinal horizontal lever effects exerted by the extrinsic limb muscles = A - B. This gives the sign of the muscle couple acting on the limb. D. Transverse horizontal lever effect calculated in a similar manner to C. There is always an adductor couple in normal walking. C and D, couples in arbitrary units. FLR, FLP, FLA, HLP, HLA: forelimb retractor, protractor and adductor and hindlimb protractor and adductor couples respectively begin to exert a larger couple than their antagonists.

a protractor couple in the forelimb. The horizontal lever effect represents the excess of one couple over the other. A very similar pattern was found in the newt. Here both fore- and hindfeet are placed about equally in front and behind the shoulder

and hip joints respectively, and the horizontal lever effect follows a pattern similar to that in the toad forelimb. In the transverse axis, the couples in both toad and newt are normally always adductor in their action and the feet are normally displaced laterally relative to the proximal limb joints. Exceptionally, however, in both toad and newt, records were obtained in which, owing to lateral turning of the body, one foot came to lie medially to its proximal limb joint; in these cases there was an abductor couple. The following generalization may therefore be made concerning the pattern of muscle activity in the toad and newt: the couple exerted on the limb by each group of extrinsic muscles is greater than that exerted by the antagonistic group when the foot is on the opposite side of the proximal limb joint to the origin of the muscles concerned.

The horizontal lever effect is, therefore, always of a sign opposite to the horizontal strut effect, so that the horizontal forces at the feet are always reduced to a low level. In the newt forelimb retractor stage (phases 0-2), however, the horizontal-longitudinal lever effect is larger than the horizontal-longitudinal strut effect, so that there is actually an accelerating rather than a decelerating force exerted on the body. Such a reversal of the horizontal force at the feet also occurs sometimes during part of the same stage in the toad. In the toad forelimb protractor stage (phases 2-4) a similar reversal of the horizontal-longitudinal force at the ground is a constant feature, the force exerted on the body being a decelerating force instead of an accelerating force. These features are probably related to the maintenance of an adequate pattern of total horizontal forces. In the newt forelimb retractor stage it is probably associated with the dragging of the tail, and in the toad protractor phase with the fact that the hindlimb exerts a persistent accelerating force.

It is notable that the pattern of couples in the cat (Manter, 1938) and man (Elftman, 1940) is basically similar in respect of the protractors and retractors, for which alone data are available. It is therefore of interest to investigate the functional reasons which may have led to the adoption of this pattern rather than any other. Gray has shown that on general principles several alternatives are possible.

Friction at the feet

In Fig. 11 four possible patterns of extrinsic muscle couples are shown diagrammatically, where *a* and *b* in each case represent the two main phases of normal walking which occur simultaneously on the two sides of the body. Other possible patterns can be regarded as rearrangements of 1 and 2 or as part of these patterns. In 1 and 2 the muscle couple is the same throughout the stride, in 3 the couples are positive when the feet are the same side of the joint as the origin of the muscle concerned, and in 4 they are positive when the feet are the opposite side of the joint to the origin of the muscles concerned. This last is the condition found in the toad, newt, cat and man. It is clear from the diagrams that only in 4 is the horizontal lever effect (*HLE*) always of opposite sign to the horizontal strut effect (*HSE*); all other patterns include stages when the muscles are more active than their antagonists, while the foot is the same side of the joint to their origin. In such a stage the horizontal lever and strut effects will be of similar sign and the resulting horizontal

force will be very large. The limiting static friction is μN , where μ is the coefficient of static friction and N is the force normal to the surface; so that if the horizontal forces rise above a certain level there will be a danger of slipping unless μ is very

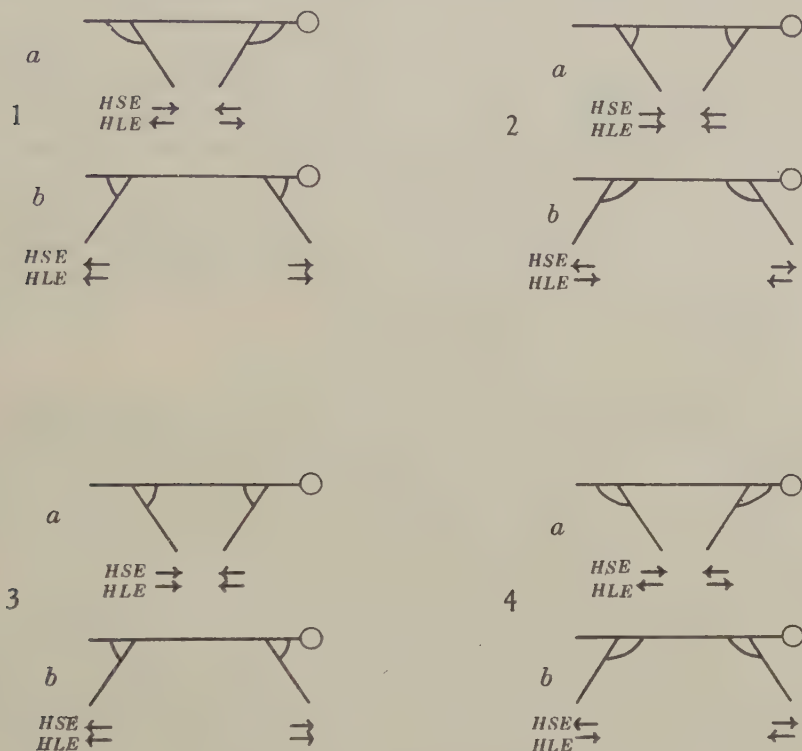


Fig. 11. Possible patterns of couples in the extrinsic limb muscles. An arc indicates that the muscle is exerting a greater couple than its antagonist. *a* and *b* of each pair of diagrams represents the simultaneous positions of the limbs of the two sides of the body in normal walking; other phases of the limbs do not differ essentially from these as far as muscle couples are concerned. Other patterns theoretically possible are impracticable on other grounds, being unstable on steep inclines. 1. The protractors of the forelimb and retractors of the hindlimb always exerting a greater couple than their antagonists while the feet are on the ground. 2. The retractors of the forelimb and protractors of the hindlimb always exerting a greater couple than their antagonists while the feet are on the ground. 3. Each group of muscles exerting a greater couple than their antagonists when the foot is the same side of the proximal limb joint to the origin of the muscles concerned. 4. Each group of muscles exerting a greater couple than their antagonists when the foot is the opposite side of the proximal limb joint to the origin of the muscles concerned. This is the condition actually found in the toad, newt, cat and man. HSE = direction of the horizontal strut effect at the foot. HLE = direction of the horizontal lever effect at the foot. Whenever the muscle exerts a greater couple than its antagonist with the foot the same side of the joint to its antagonist, the horizontal strut and lever effects are of the same sign and the horizontal forces at the feet are therefore high. Of all the possible patterns only in that shown in 4 are they always of opposite sign and the horizontal forces at the feet consequently always low.

high. That the coefficient of static friction is in fact often low is suggested by the fact that the feet of newts and toads will sometimes slip towards the end of their strokes on wet surfaces. It is therefore probable that the pattern shown by the toad

and newt, being the only one in which the horizontal lever effect is always of opposite sign to the horizontal strut effect, is a fundamental adaptation to the conditions of low friction under which these animals habitually live; it is probably also the only one possible for the earliest terrestrial tetrapods.

Support of the body

The couple exerted on the limbs by the extrinsic muscles has a vertical as well as a horizontal effect (Gray, 1944). The pattern of couples found in the toad and newt tends to increase the support of the body by the limbs, but in all other patterns there will be stages (when muscles are active while the foot is the same side of the proximal limb joint to their origin) in which the vertical effect of the couple will tend to reduce the vertical support given by the limb and so place an extra strain on the intrinsic muscles of the limbs. The pattern actually found is therefore, in this respect also, the most economical possible.

Resistance to external forces

The two features described above lead to the conclusion that this pattern is the best adapted to withstanding external forces which may be applied to the animal and is that which is best adapted to progression on steep inclines. In order to resist a horizontal force increased tensions must be exerted by the extrinsic limb muscles, and in all other patterns this would lead at some stage to greatly increased horizontal forces at the feet. A weight placed on the back would have a similar effect by increasing the horizontal strut effect and would also place a very large strain on the intrinsic muscles during phases in which the vertical support is reduced. On a steep incline the force tangential to the ground is greatly increased in some positions of the limbs and would lead to slipping if the horizontal lever effect were of the same sign. It is therefore unlikely that any animal could be used for draught or pack purposes if the pattern of muscle couples on its limbs were not of the type found in the toad, newt, cat and man. The use of a number of widely different animals (e.g. camel, elephant, dog, horse, yak and goat) argues strongly in favour of this pattern being, at least in general outline, common to all tetrapods.

Standing

Toads and newts rarely stand with their bodies entirely off the ground, but when only part of the weight was carried by the limbs, records obtained from standing animals always showed a pattern of extrinsic muscle couples identical with that observed in walking. This is not surprising, since the mechanical considerations just discussed apply equally to standing and walking. It seems probable, therefore, that this pattern is generally adopted in standing, and the muscles are rested in turn by changing the positions of the limbs.

Lateral bending of the back

Gray showed that the extrinsic limb muscles have an effect on the lateral bending of the back. In Fig. 12A the horizontal forces acting on the body and ground as a result of the action of the limbs as struts are shown. Those due to the action as

transverse struts are transverse compressions and do not affect this feature, but those due to the action of the limbs as longitudinal struts tend to rotate the limb girdles in a horizontal plane and so place a strain on the lateral longitudinal muscles of the back. In Fig. 12A the strain falls on the muscles of the left side. An extrinsic muscle exerts equal and opposite couples on the limb and body (Gray, 1944), so that, if the extrinsic muscles were to contract in the pattern found in the toad and newt to such an extent as to reduce the horizontal forces at the feet to zero, the strain on the body due to the strut effect would be removed. In the Amphibia, owing to the lateral displacement of the limbs and therefore of the extrinsic muscle

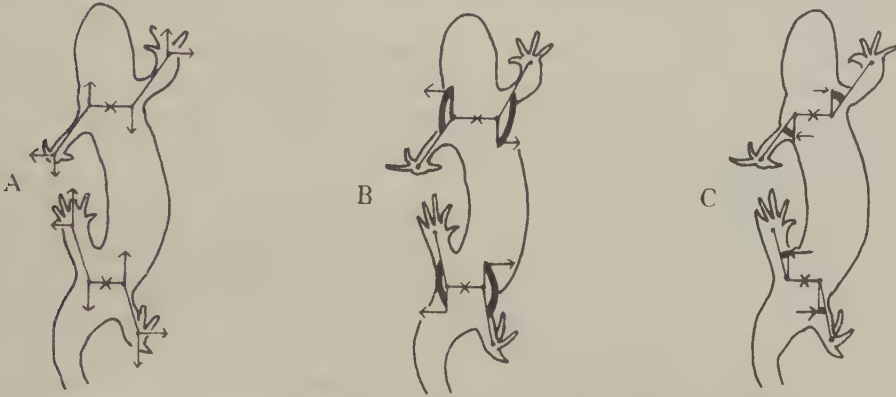


Fig. 12. Effect of the extrinsic limb muscles on the lateral undulations of the body. A. Limbs acting simply as struts; no extrinsic muscles active. The transverse horizontal strut effects cause only transverse compressions, but the longitudinal-horizontal strut effects cause equal and opposite forces acting on the body and ground, the former tending to rotate the girdles horizontally in a manner opposing the lateral undulations shown in life. B. Muscles active in the manner found in the toad and newt. The horizontal lever effect is equal to the horizontal strut effect so that the horizontal forces at the feet are reduced to zero and the tendency to rotate the girdles shown in A is abolished. But, in addition, owing to the lateral displacement of the limbs and therefore of the insertions of the extrinsic limb muscles, these muscles tend to rotate the girdles in a manner precisely opposite to A, tending to bring about the lateral undulations of the body shown in life. C. Muscles exerting a greater couple than their antagonists when the feet are the same side of the proximal limb joint to the origin of the muscles concerned (Fig. 11 (1b), (2a), (3a) and (3b)). The horizontal strut effects are not shown but remain as in A and, in addition, the effect of the muscle couples is to tend to rotate the girdles in a manner opposite to B and similar to A, i.e. further to oppose the lateral undulations of the body shown in life.

insertions, it would be replaced by an exactly opposite strain due to the action of the extrinsic muscles (Fig. 12B). On the other hand, in any other pattern, during the stages with an increased horizontal force at the feet, the effect of the extrinsic muscles is to increase that strain on the lateral body musculature which would be caused by the horizontal strut effect alone (Fig. 12C). Urodele amphibians and many reptiles exhibit a regular pattern of lateral undulations of the body during normal walking. The longitudinal strains shown in Fig. 12A and C would tend to oppose these movements of the body and would therefore make large muscular efforts necessary. On the other hand, the strains shown in Fig. 12B tend to cause just such a pattern of lateral undulations as is found in life. It has, however, been

shown that the forces exerted on the ground are not reduced to zero but only to a small fraction of the horizontal strut effect. The actual condition in a urodele must therefore be intermediate between Fig. 12A and B, with small horizontal forces at the feet, tending to oppose the lateral bending, and rather larger muscle couples tending to bring it about. This is confirmed by the fact that as newts increase their speed of progression, and hence of muscle activity, the lateral undulations of the body are usually increased in magnitude. It therefore seems clear that the lateral undulations of the body in urodeles are brought about, at least in part, by the extrinsic limb muscles. No other pattern of muscle activity would do this. Since these undulations in conjunction with the lateral displacement of the feet lengthen the stride considerably (Schaeffer, 1941) they are probably of functional advantage. This muscle pattern is therefore in this respect also the most economical possible. In the toad the same undulations occur, but in reduced form (seen most clearly in cine-X-ray photographs), probably because the feet are relatively less displaced laterally than in the newt. The natterjack toad shows greater lateral undulations than the common toad.

In the cat and other mammals the feet are almost in the same vertical longitudinal plane as the proximal joints of the limbs, so that lateral undulations of the body would lengthen the stride extremely little and would not be of any appreciable functional advantage. Also the extrinsic muscle tensions act almost in the same plane and so have very little tendency to rotate the girdles horizontally while the actual horizontal forces at the feet are probably always small. It is, therefore, not surprising to find that the lateral undulations are in fact reduced to very small proportions in nearly all mammals.

Vertical bending of the back

Gray has also shown that the extrinsic muscles tend to arch or sag the back and so affect the work done by the muscles which support the weight of the body along the vertebral column. In Fig. 11 (1) and (2) the tendency is to arch and sag the back respectively; at high speeds of locomotion, when the extrinsic muscles are very active, the type of strain placed on the back muscles is profoundly affected, and special and prolonged muscular effort is necessary to counteract them. In Fig. 11 (3) and (4), however, the muscles of the two sides of the body have opposite effects to each other, so that the total effect on the vertical bending of the back is negligible and will not be affected by the degree of activity of the limb muscles, although torsional strains might be introduced. Even the most rapid locomotion therefore need not place any significant strain on the vertebral muscles (other than those resisting torsion) so long as the diagonal pattern of limb movements is maintained. In standing, an equitable distribution of effort on the part of these muscles would again be better obtained by alterations in the positions of the limbs than by alterations in the type of muscular pattern. These conclusions would hold whether the weight of the body tends at rest to arch or to sag the back, and therefore apply equally to all types of tetrapod.

VI. THE INTERNAL MECHANICS OF THE TOAD FORELIMB

The humerus of the toad with the insertions of its most important muscles is shown in Fig. 13. The articular head has, on its ventral surface, two ridges separated by a groove which corresponds to a ridge in the lip of the glenoid cavity. When the humerus is fully protracted these structures fit together closely and the humerus is effectively prevented from rotation about its own longitudinal axis. As the humerus is retracted, however, the shallower regions of the groove on the head come to lie against the lip of the glenoid, and the bone has progressively greater freedom to rotate. This 'locking' mechanism only operates if the humerus is held firmly in the

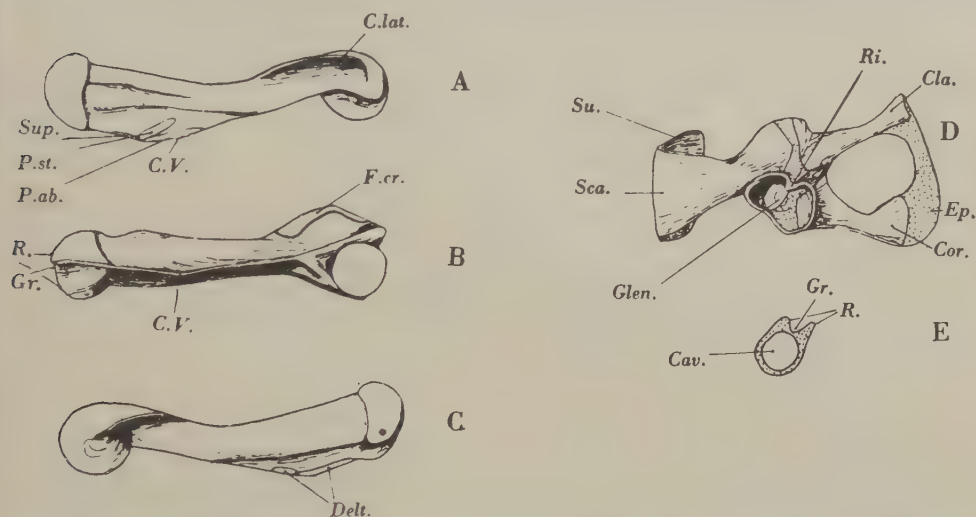


Fig. 13. The humerus and shoulder joint of the toad. Male specimen measuring 2.15 in. from snout to tip of the urostyle. A, B and C. Posterior, ventral and anterior aspects respectively of the right humerus. Actual length 2 cm. D. Ventral view of the right shoulder girdle of the same toad as A. E. Transverse section of the proximal articular end of the humerus where it fits into the glenoid cavity. The groove (*Gr.*) corresponds to the ridge (*Ri.* in D) in the glenoid cavity, so that when the humerus is protracted it is completely prevented from rotating about its own axis. *C. lat.* crista lateralis. *Cav.* central cavity of humerus. *Clav.* clavicle. *Cor.* coracoid. *C.V.* crista ventralis humeri. *Delt.* insertion of *m. deltoideus*. *Ep.* epicoracoid cartilage. *F. cr.* insertion of *m. flexor carpi radialis*. *Gr.* groove on articular head of humerus. *Glen.* glenoid cavity. *P. ab.* insertion of *m. pectoralis p. abdominalis*. *P. st.* insertion of *m. pectoralis p. sternalis*. *R.* ridges on head of humerus. *Ri.* ridge in glenoid cavity. *Sca.* scapula. *Su.* suprascapula. *Sup.* insertion of *m. supratoracoides*.

glenoid cavity, as would be the case in life. The humerus is, however, free to move antero-posteriorly in a horizontal plane, and during the stride it is retracted through an angle of about 90° when seen from above. The relative movements of the limb segments can be seen from Fig. 2. As well as being protracted and retracted the humerus is adducted slightly, so that its distal end moves along a line inclined upwards and backwards relative to the long axis of the body. By this means the glenoid cavity is maintained at a fairly constant level above the ground. The radio-ulna is flexed and extended on the humerus in such a way that the lateral distance of the foot from the glenoid cavity remains fairly constant also, thus ensuring a

fairly steady walk. In addition to these movements the radio-ulna rotates about the long axis of the humerus rather as the spoke of a wheel rotates about its axle.

This rotation of the radio-ulna about the long axis of the humerus might be due, either to its rotation about the fixed end of the humerus (= *elbow rotation*), or to the rotation of the humerus and radio-ulna together, involving no movement in the elbow joint (= *humerus rotation*). From measurements of the rotation of the humerus, carried out as described, the part played by those two elements was calculated and the results are shown in Fig. 14. So long as the humerus is in front of a line at right angles to the long axis of the body it does not rotate at all (phases $5\frac{1}{2}$ -1). This

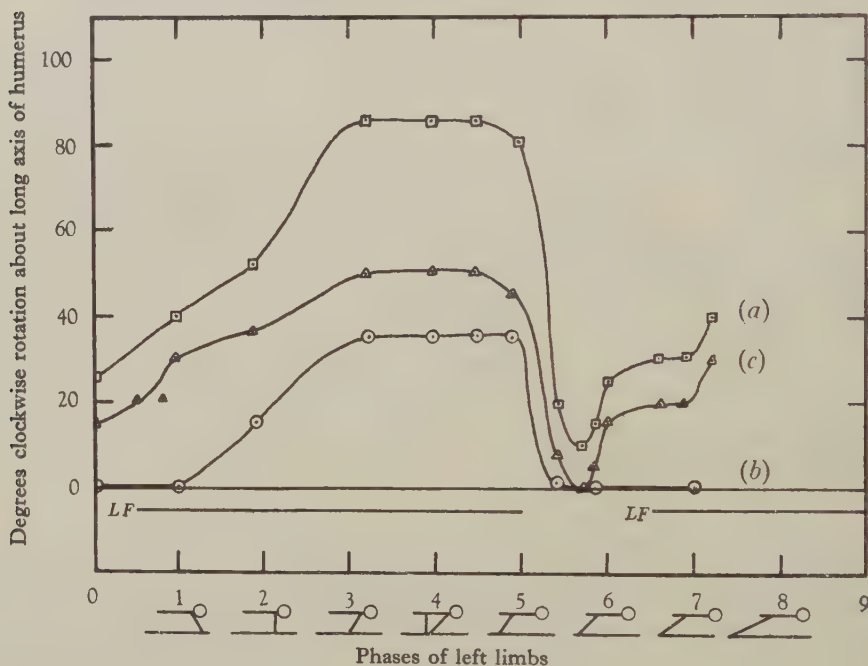


Fig. 14. Rotation about the long axis of the humerus of a toad. Ordinates, degrees clockwise rotation about the long axis of the humerus from an arbitrary zero position; as seen from the right side. The line *LF* represents the periods when the limb concerned (the left forelimb) is in contact with the ground. In order to avoid confusion the values of (a) are given as 10° higher than those actually recorded. (a) Total rotation of the hand about the long axis of the humerus as measured from the photographs. (b) Humerus rotation. Measured simultaneously with (a) from the movements of a pin inserted in the humerus. (c) Elbow rotation. Calculated from (a) and (b) above. $(c) = (a) - (b)$.

accords well with the shape of the joint, which should be completely locked at this stage. After phase 1 sufficient retraction has taken place to allow a certain amount of rotation in the joint and the humerus is progressively rotated as it is retracted. Elbow rotation takes place at the same time according to a very similar pattern, except that during phases $5\frac{1}{2}$ -1, when the humerus is locked, there is considerable elbow rotation, first bringing the foot down on to the ground and later, in phases $\frac{1}{2}$ -1, helping to propel the body forwards.

The rotation of the radio-ulna about the humerus greatly increases the length of the stride, and in normal walking the distal end of the humerus moves through only about one half of the distance traversed by the foot. Such a movement, however, involves certain mechanical difficulties.

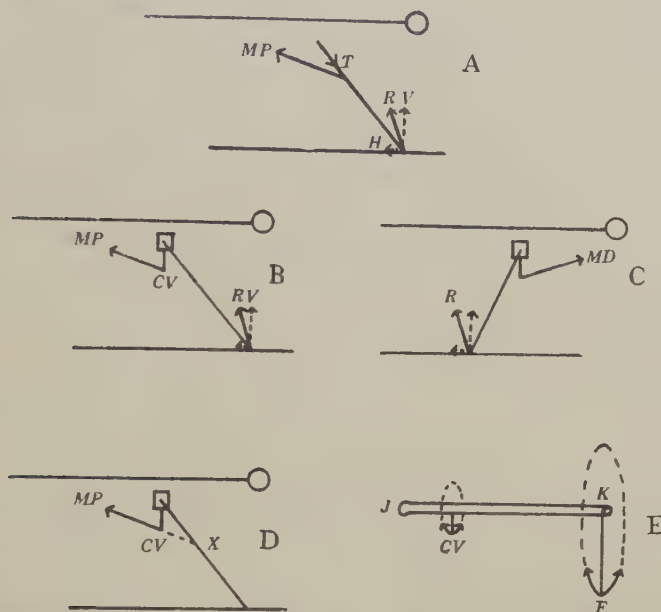


Fig. 15. The internal mechanics of the toad forelimb. A. Theoretical limb moved in the same vertical longitudinal plane as the shoulder joint. The m. pectoralis (MP) is active and the total effects on the limb are a longitudinal compression and a transverse bending strain. R =reaction at foot. V and H =vertical and horizontal components of this reaction. T =thrust along limb axis. B and C, the toad. The humerus (square) is seen in end view as it projects horizontally and laterally from the body with the crista ventralis (CV) ventral. The elbow joint is regarded as rigidly fixed. B. Limb acting as a lever when the m. pectoralis is exerting a greater couple than its antagonists. The horizontal force at the foot is reduced and the reaction (R) tends to rotate the limb in an anticlockwise direction. This rotation is opposed by the clockwise couple exerted by the m. pectoralis owing to its insertion on the crista ventralis. C. Limb acting as lever as in phase 3, when the couple due to the m. deltoideus (MD) is large enough to reverse the sign of the horizontal force acting at the foot. The reaction at the foot therefore has a considerable clockwise couple on the limb and would have even if the foot were directly under the humerus. A balance similar to that in B is maintained by the direct anticlockwise couple due to the m. deltoideus acting on the crista ventralis. D and E. The mechanics of the 'double crank' limb. D. Side view as in A. The total effect on the limb is the same as if the m. pectoralis was inserted on the radio-ulna at X , and similarly for the m. deltoideus. As it is, however, large torsional strains fall on the limb between X and CV . E. Viewed from behind and to the side. The member JK (the humerus) rotates about its long axis owing to the horizontal forces applied at CV ; this causes the point F to rotate also and to exert tangential forces against any resistance. If forces of opposite sign were applied at CV and F a torque would be applied to JK . In life the main extrinsic muscles are inserted on the limb at a point corresponding to CV and the foot corresponds to F . The term 'double crank' is appropriate because reciprocal motion at CV is translated into rotary motion and then back again into reciprocal motion at F .

Regarding the limb as a rigid rod hinged at the shoulder the reaction at the foot (R in Fig. 15) will exert an anticlockwise couple on the limb (seen from the right side) before phase 2 and a clockwise couple after phase 2. (Even when the foot does not lie much behind the axis of the humerus after phase 2 the horizontal force

at the foot is a retarding force giving a clockwise couple of appreciable magnitude.) The *m. pectoralis* is more active than its antagonists before phase 2 and the *m. deltoideus* after phase 2, and these muscles exert respectively clockwise and anticlockwise couples on the limb owing to their insertion. They will therefore produce couples always of opposite sign to those due to the reaction at the ground. This is explained by the fact that the muscle tensions are responsible for reducing the horizontal forces at the feet and so producing the couples due to the reaction at the ground.

If the limbs were moved only in the same vertical longitudinal plane as the shoulder joint (as in the mammals), the large forces acting on the limbs would all lie in this plane. The strains acting on the limb in this case would be only a compression and a bending strain (Fig. 15 A). In the toad, however, the limbs project laterally and the main extrinsic muscles are inserted on the *crista ventralis*. In side view, therefore, the toad forelimb must be regarded as in Fig. 15 B, C. In addition to a bending strain on the limb there is a torque between the elbow and the insertion of the extrinsic muscles. Unless the elbow joint gives way to this, and Fig. 14 shows that it does not, this will fall as a torque on the humerus itself.

The fundamental mechanism of the limb may therefore be compared, in mechanical terms, to a double 'crank', as in Fig. 15 D and E. The member JK rotates about its long axis owing to rectilinear forces applied at CV (cf. *crista ventralis*). The rotation is again transformed into rectilinear motion (actually tangential in the diagram) at F (cf. the foot). In addition to this 'crank' movement the humerus is of course retracted through an arc in the horizontal plane. The whole limb movement differs from that in the mammals therefore, not only in that the humerus is retracted in a horizontal rather than a vertical-longitudinal plane, but also in that a movement of rotation about the longitudinal axis of the humerus plays a fundamental part in the stride. The mechanism is readily clarified by the use of a card-board model.

In order to test this analysis parts of the *m. pectoralis* were paralysed and the rotation of the humerus measured as before. The results are shown in Fig. 16. Paralysis of the *m. pectoralis* probably results in a compensatory increased tension in other retractors. These do not exert such a large rotary couple on the humerus, since they are not inserted on the *crista ventralis*, but they nevertheless reduce the horizontal forces at the feet in the same way as the *m. pectoralis* owing to their function as retractors. The observed reduction of the amount of clockwise rotation is, therefore, what should be expected, and the lack of any change during the early phases of the stride is presumably due to the locking mechanism in the joint limiting the movement forcibly.

Any forcible limiting of the rotation of the humerus by the joint surfaces will involve mechanical shearing forces acting on the articular ridges. It is, however, generally believed that, in mammals at least, the limiting of movement in joints is performed by muscles and ligaments and the articular surfaces carry only compression forces. In order to test the normal function of the locking mechanism the articular ridges were shaved off the head of the humerus in a number of toads. Normal walking was restored in about two months and was apparently unaffected

by the operation, while the ridges were not regenerated. Since also the ridges consist only of calcified cartilage it seems unlikely that in normal walking there are appreciable shearing forces in the joint. The function of the locking mechanism is probably to act as a guide to the humerus and so ensure a correct rotation of that bone. A proper degree of rotation of the humerus is very important because, owing to the displacement of the insertion of the main muscles from the long axis of the bone, a small rotation makes a considerable difference both to the effective distance of these muscles from the joint and to their length. These factors are particularly

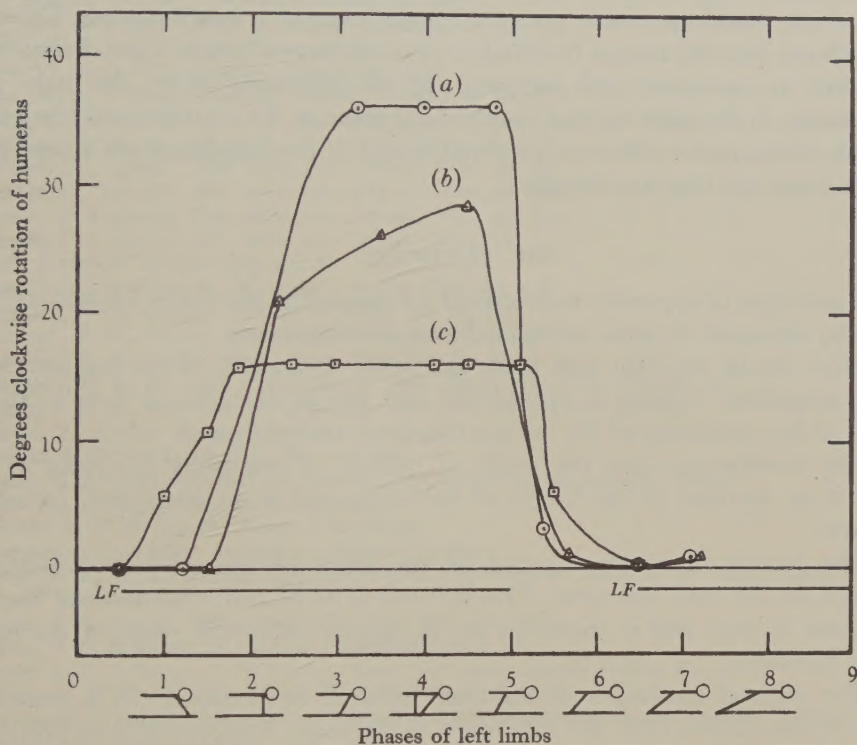


Fig. 16. Effect of paralysis of the *m. pectoralis* on the rotation of the humerus. As in Fig. 14. (a) Normal (same as Fig. 14b). (b) After section of the *n. pectoralis proprius*. (c) After section of the *m. pectoralis p. abdominalis*.

important when the foot is first placed on the ground, and it is noteworthy that it is then that the locking mechanism acts most effectively. Probably this guide mechanism comes into action actively when the animal walks over very rough ground, and in these conditions there may be shearing forces in the joint. These experiments therefore fit in well with the mechanical analysis already given.

In conclusion then, we may say that some device such as the 'crank' mechanism is essential to the operation of the limb as an active lever with the humerus moving in a more or less horizontal plane. If the limb were to act only as a strut the whole mechanism could be much simpler, but the limb does not act only as a strut, and

in practice the 'crank' mechanism also makes possible a considerable increase in the length of the stride.

The newt shows, in both fore- and hindlimbs, a pattern of muscle couples essentially similar to those of the toad forelimb, and also similar movements and morphological features. It is clear that both limbs are of the 'crank' type. The studies of Watson (1917 especially) and a comparative study of living and extinct Amphibia and reptiles strongly suggests that this type of limb is common to all the lower tetrapods apart from a few secondarily aquatic types. The extremely massive humeri of many large extinct forms are probably related to the very large torsional strains which would have been placed on these bones in a heavy animal. There is good evidence that the anuran hindlimb is derived from a 'crank' type of limb but is modified in connexion with jumping. In the mammals where the limbs are moved almost in the same vertical-longitudinal plane as the shoulder and hip joints the whole mechanism is different, torsional strains of any magnitude are absent and the limb bones are long and slender.

VII. SUMMARY

1. A new type of apparatus is described for measuring the forces exerted on the ground by tetrapods in three orthogonal axes simultaneously.

2. From results obtained with toads and newts an analysis of the mechanics of normal amphibian walking is carried out and several features of Gray's (1944) analysis of the mechanics of the tetrapod skeleton are confirmed.

3. The introduction into the stride of periods of instability is shown to be related to an increase of the length of the stride and is an adaptation to faster movement.

4. The pattern of couples exerted on the limbs by the extrinsic muscles is calculated for the toad and newt. This is found to be basically the same as that in the cat and in man and is shown to be, in several important respects, the most efficient possible.

5. The internal mechanics of the toad forelimb is discussed. It is basically similar to that of both fore- and hindlimbs of the newt. The operation of this type of limb is compared to that of a 'crank' mechanism and differs in important respects from that of the mammals.

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